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CONTRIBUTIONS TO THE GENETICS OF CERTAIN CHROMOSOME ANOMALIES IN DROSOPHILA MELANOGASTER

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KNOWN AND PROBABLE INVERTED SECTIONS OF THE AUTOSOMES OF DROSOPHILA MELANOGASTER

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With three text-figures

CONTENTS

I

KNOWN AND PROBABLE INVERTED SECTIONS OF THE AUTOSOMES OF DROSOPHILA MELANOGASTER

INTRODUCTION

Early in the study of linkage in *Drosophila* there were found several cases of crossover reducers, whose effect was noticeable only when they were heterozygous. These have been studied more or less continuously since they were first discovered, but for several years little progress was made in interpreting them. In 1921, as a result of studies on linkage in *simulans*, I suggested (Sturtevant, 1921) the possibility that such crossover reducers might be inverted sections of chromosomes; but at that time the suggestion could not be tested. In 1924 I undertook a systematic search for new examples of crossover reducers, in the hope that cases more favorable for analysis might be found. The present paper is a report of the results of that search and of a study of the new reducers found and of the previously known ones. The study has yielded a positive result—several of the reducers actually are inverted sections as suggested (Sturtevant, 1926).

The work on which this paper is based was supported by Carnegie Institution of Washington.

TESTS OF WILD STOCKS

It seemed desirable to get some idea of the relative frequency of different types of crossover reducers in unrelated stocks and to get further data bearing on the question of a possible correlation in occurrence of different reducers. It was also hoped that systematic study might lead to the discovery of new types of reducers, which might be favorable for study or useful in other ways.

Wild stocks were obtained from widely separated localities and were tested as soon after collection as possible, though in some cases stocks that had been in the laboratory for two or three years were used. Many friends have helped by collecting such wild stocks.[1] None of the tests were carried out on a large scale, with the result that reducers might be present in a tested stock without being discovered. The data obtained are valid where they give positive results, but not where they give negative ones. Further, the tests given the different strains were not equally extensive. The Woodbury, Connecticut, stock, for example, was tested for chromosome III three times, whereas most other strains were tested only once for a given chromosome. It may be noted also that a crossover reducer was found in one of these tests of the Woodbury stock, but was not recovered in either of the other tests. One may safely conclude that more extensive tests would have shown reducers to be present in some of the other stocks in which they were not found.

[1] Dr. D. E. Lancefield and Dr. H. H. Plough may be especially mentioned as having each furnished a number of stocks from different localities.

detailed counts were made only for the offspring emerging in the first few days. As soon as a culture could safely be classified as giving normal crossover values it was discarded. All cultures with reduced values were kept for complete counts, and the data from all such counts will be found in this paper. The data from such "normal" cultures as were carried to completion have, however, not been recorded here.

Table 1 gives the results of these tests. The + sign signifies that a chromosome substantially normal for the region concerned was recovered. All the other symbols indicate the recovery of some type of powerful reducer. Discussion of the nature of these various reducers, their relation to each other, and their geographical distribution may most conveniently be taken up later in this paper. We may note here that, while reducers are by no means rare, at least in chromosomes II and III, normal chromosomes were found present in all but two cases and are clearly much the most common. The two exceptional cases are the stocks from Columbia, Missouri, and Ensenada, Porto Rico, from neither of which was a normal right limb of chromosome III recovered. Neither stock was extensively tested; and it is important to add that each is known to have been reduced to a single fertilized female at one period in its history before testing, so that neither can be considered to represent a fair sample of the original wild population concerned.

Reference to the literature shows relatively few definite records of tests of chromosomes from known wild sources. The cases I have been able to find are summarized in table 2.

TABLE 2—*Published records of tests of wild stocks for crossover reducers*

Stock	IIL	IIR	IIIL	IIIR	Authority
Amity, Ore.	..	..	+, N	+	Bridges and Morgan, '23; Bridges, unpubl.
Ann Arbor, Mich.	Cy	Cy	..	..	Ward, '23
Austin, Tex.	..	..	+	+	Payne, '24
Bloomington, Ind.	..	..	+, N	+, P	Payne, '24
Camp Jackson, S. Car.	..	..	+	+	Strong, '20; Bridges and Morgan, '23
Falmouth, Mass.	..	+	..	..	Plough, '17
Harris, Minn.	..	..	..	+	Bridges and Morgan, '23
Liverpool, Nova Scotia	N	+, N	..	..	Sturtevant, '19
Mitchell, S. Dak.	..	..	..	+	Bridges and Morgan, '23

CROSSOVER REDUCERS FROM SOURCES OTHER THAN TESTED WILD STOCKS

The study of the relations of various crossover reducers to each other was planned to include all the powerful autosomal types available. Several of those used have already been recorded more or less fully. These are as follows: C II L Cy and C II R Cy (Ward, 1923); C II L N and C II R N (Sturtevant, 1919); C III R E (Muller, 1916); C III L P and C III R P (Payne, 1924); C III L o and C III R o (Morgan, Bridges and Sturtevant, 1924); C III L M and C III R M (Morgan, Bridges and Sturtevant, 1924). In addition two new forms were used that have recently been found in mutant stocks but have

not been reported up to now: C II L T (from III-ple stock), and C III R sbd (from black jaunty stock).

C'S IN RIGHT LIMB OF CHROMOSOME III

The right limb of chromosome III has been more thoroughly studied with respect to crossover reducers than has any other region. This is because C III R's have been found most frequently, and also because they have proved easier to analyze. Accordingly the data obtained from their study will be presented in some detail, the other types being discussed later and more briefly in this paper.

Three classes of C III R's have been found, of such a nature that a fly heterozygous for any two belonging to the same class (or homozygous for any one) shows a total crossing over in the right limb of chromosome III not very different from that found in a homozygous "normal" fly (*i. e.*, one carrying no C); while a fly heterozygous for any two belonging to different classes gives at most no more crossing over than if it were heterozygous for only one.

There is evidence, as will appear later, that all these C III R's are really inverted sections. A catalogue of them follows, the terminology used being based on the evidence that they are all inverted sections.

IN E

The first linkage discovered in the third chromosome was that between pink and ebony (Sturtevant, 1913). The data obtained indicated great variations in linkage, but these were not understood until Muller (1916) showed that there was a crossover reducer present in the ebony stock and in certain related stocks (beaded, spread, eosin). Muller showed also that this C III R gave high crossover values when homozygous, as was already known for C II R N. Muller showed further that spineless ebony gives a higher value in homozygous C III R E than in homozygous normal flies, but the significance of this result was not understood until the work with an allelomorph of C III R E (C E^{Pr}) led to the discovery (Sturtevant, 1926) that both of these C's are inversions, which we may designate as In E and In E^{Pr}, respectively.

The experiments here reported involve the original inverted section from the ebony stock and those from the beaded (see Muller, 1918) and eosin (see Sturtevant, 1919) stocks, both of which probably have the same origin as the ebony one, since all three trace to the same original stocks. These stocks were collected either near New York City or near Woods Hole, Massachusetts, about the year 1909.

IN E^{Pr}

This inversion was found in a wild stock that was collected at Prague, Czechoslovakia, by Dr. A. Brozek, in 1925. There were also present in this stock third chromosomes that gave the usual crossover relations. As already reported (Sturtevant, 1926), tests showed that this is an inverted section and that it is allelomorphic to In E.

IN Mo

This inversion was found in a wild stock collected in 1924 at Columbia, Missouri, by Dr. W. R. B. Robertson. Two different tests of this stock were

made (against III-ple); in one case six and in the other case seven F_1 females were tested, and all carried the inversion. Apparently the Missouri stock was homozygous for In Mo, but it should be added that this stock was known to be descended from a single fertilized female, so that it did not contain a fair sample of the third chromosomes from the region where it was collected.

Tests to be described below have shown that In Mo is probably an inversion, the best evidence coming from the crosses with In Mo^{NO}. This represents a new class of inversions, no member of which has hitherto been recorded.

IN Mo^{B}

Dr. F. Schrader collected a wild stock at Bryn Mawr, Pennsylvania, in 1925. The present inversion, together with normal third chromosomes, was found in this stock. Tests showed (see below) that it was allelomorphic to In Mo. It showed no specially interesting characteristics and has been discarded.

IN Mo^{NO}

This inversion was found in a stock collected in 1926, by Dr. C. I. Bliss, at New Orleans, Louisiana. A weak allelomorph of ebony, known as ebony-12 (e^{12}) was present in this chromosome, in the region where the crossover reducer is most effective. This fact made it possible to show clearly that the New Orleans reducer is allelomorphic to the Missouri one, and also to make it probable that both are inversions (see data in this paper on In Mo/In Mo^{NO}).

IN P

Payne (1924) recorded the occurrence of a crossover reducer in the right limb of some (but not all) third chromosomes of a stock from Bloomington, Indiana. I have found this reducer to be allelomorphic to two of the recorded C III R's, and also to six new ones found in the course of the present study. Due in part to the discovery (by Mr. Shlaer) that "orange" eye-color (described by Bridges as associated with a C III R) is allelomorphic to cardinal, it has been possible to demonstrate that the Payne series of C III R's are inversions. This evidence will be presented later in this paper.

IN P^{Ci}

This was found in a wild stock collected in 1926 at Cienfuegos, Cuba, and received through Dr. G. H Parker. Normal third chromosomes were also present in the stock. Like In P^{G}, it was shown to be allelomorphic to In P^{sbd} and was then discarded.

IN P^{En}

This inversion was found in a wild stock that was collected in 1925 by Dr. J. S. Dexter at Ensenada, Porto Rico. Two different tests of this stock were made; in each case five F_1 females (from crosses to III-ple) were all heterozygous for In P^{En}. The stock had previously been reduced to a single fertilized female, so it is quite possible that it had originally contained normal third chromosomes. This inversion was shown to be allelomorphic to In P^{sbd}, and therefore to belong to the Payne series.

IN P^F

This inversion was discovered by Mr. H. D. Fish in a wild stock collected in 1925 by Dr. D. E. Lancefield at Olympia, Washington. I had carried out a routine test of this Olympia stock, without recovering any crossover reducer; but soon afterward Mr. Fish, in using the stock for certain linkage experiments, found a chromosome that contained both a C III L and a C III R. This C III R, shown to belong to the Payne inversion series, has been used in several experiments, as will appear below.

IN P^G

This was found in a stock collected in 1926 by Mr. D. Burdick at Georgetown, Texas. A single routine test showed three kinds of third chromosomes to be present in this stock: one normal, one with a C III L and one with a C III R. The C III R was shown to belong to the Payne inversion series and was then discarded.

IN P^M

This is listed by Morgan, Bridges and Sturtevant (1924) as "C III R. L. V. Morgan." Mrs. Morgan discovered it in working with certain mutant strains. I have studied it only enough to make sure that it belongs to the In P series of allelomorphs.

IN P^o

This inversion was found by Bridges in working with a mutant eye-color called orange, and was found always to be present when the orange eye-color was present. Mr. S. Shlaer found the same eye-color independently (almost certainly from the same source as Bridges' strain), and found likewise that it was associated with a C III R. Mr. Shlaer further found that orange is an allelomorph of cardinal, and this discovery made it possible to compare the locus of cardinal in the normal map with that in homozygous Payne-allelomorph C III R females. The result shows that these C III R's are inverted sections.

IN P^{sbd}

In looking over the black jaunty stock made up by Clausen (Clausen, 1924), I found a few flies closely resembling the mutant type known as stubble. These flies were also black jaunty, and were therefore not due to contamination. Tests showed that the new character, known as stubbloid, is due to a recessive third chromosome gene, ultimately found to be allelomorphic to stubble, which is dominant. Associated with stubbloid was found a C III R, only separable from it with great difficulty; and this C III R has been found to be an inversion allelomorphic to In P.

IN P^W

This inversion was found in a wild stock which I collected in 1924 at Woodbury, Connecticut. There were apparently more normal third chromosomes than In P^W in this stock when it was tested as, in three separate tests, two gave no In P^W and the third gave both normal and In P^W. There has always been a lethal associated with this inversion, so it has not been tested in homozygous form. There is abundant evidence that it belongs to the In P series, as will appear below.

CROSSING OVER IN FEMALES HETEROZYGOUS FOR C III R'S

Tables 4 to 12 show the results obtained from females heterozygous for the various C III R's. These data are summarized (in part) in table 3. It is obvious at once that there are irregularities and inconsistencies (for example, that In P^{Ci} gives st ss 17.3, while st sr is only 9.8, though it includes all of the st ss section). These are presumably of the same nature as the minor variations noted by Bridges and Morgan (1923). They make it impossible to use table 3 for detailed analysis of the situation, for which the raw data of tables 4 to 12 must be used. Even these data are in many experiments seriously affected by differential inviability. Nevertheless the very striking reductions in crossing over due to the C's are unmistakable. It is not certain that any of the

TABLE 3—*Summary of crossover values for In/+*

	ru hy	ru st	D st	th cu	st p^p	st Sb	st ss	st sr	p^p ss	cu sr	Sb sr	ss e	sr e	e ro	ro ca
In E (beaded)	....	....	....	....	....	....	....	14.5	....	....	....	....	0	0	0
In E (ebony)	....	....	....	....	....	....	....	4.5	....	....	....	....	0.1	0	0
In E (eosin)	....	....	....	....	....	....	....	10.8	....	....	....	....	0.1	0	0
In E^{Pr}	....	45.9	....	8.3	5.1	....	7.0	10.1	1.9	4.8	...	0	0.1	0.01	0.01
In Mo	....	42.2	3.1	....	3.6	9.2	3.9	9.0	0.4	....	0.1	0	0.1	0	0
In Mo^B	....	42.2	....	....	3.0	....	3.0	9.0	0.4	....	...	0	0	0	0
In Mo^{No}	....	39.1	....	11.8	3.0	....	4.5	....	1.5	4.4	...	0	0.1	0	0
In P	....	....	....	....	....	....	....	7.6	....	....	....	....	0	0	0.2
In P^{Ci}	....	45.5	....	....	16.1	....	17.3	9.8	1.8	....	...	0	0	0	0.3
In P^{En}	....	44.5	....	....	4.0	....	4.8	6.5	0.8	....	...	0	0	0.1	0.2
In P^{G}	....	38.0	....	....	2.7	....	2.7	8.3	0	....	...	0	0	0	0.1
In P^{o}	....	....	....	....	....	....	....	8.4	....	....	....	....	0	0.1	0.5
In P^{sbd}	....	....	....	....	....	8.2	....	5.5	....	....	....	....	0	0	0.4
In P^{W}	....	45.3	....	....	6.0	....	6.5	10.0	0.6	....	....	0	0	0	1.1
CLF In E	0	0	....	....	....	....	....	15.6	....	....	....	....	0.1	0	0
CLP In E	0	0	....	....	....	....	....	9.0	....	....	....	....	0.4	0	0
CLP In Mo	0	0	....	....	....	....	....	20.1	....	....	....	....	0.3	0	0
CLF In P	0	0	....	....	4.5	....	8.2	....	4.2	....	....	0	....	....	....
CLG In P	0.1	0.1	....	8.2	....	....	....	7.2	....	2.6	....	....	0	0.1	1.6
CLP In P	0	0	....	....	0.9	....	2.1	6.1	1.3	....	...	0	0	0.2	0.8
CLF In P^{F}	0	0	....	1.1	1.4	....	2.7	2.3	1.5	0.3	...	0	0	0.01	0.3
CLo In P^{o}	0	0	....	....	3.8	....	6.5	....	3.1	....	....	0	....	....	....
Standard (+/+)	25.6	40.7	3.6	7.3	4.0	13.1	13.4	16.5	10.1	11.7	3.8	12.2	8.7	20.3	9.6

TABLE 4—*Tests of CIII's against ru hy st sr e^s ro ca*

CIII tested	0		3		4		5		6		3, 5		3, 6		1, 2, 5		Total
CLF In E	637	520	106	106	0	1	0	0	0	0	0	0	0	0	0	0	1370
CLP In E	591	520	56	54	4	1	0	0	0	0	0	0	0	0	0	0	1226
CLP In Mo	651	614	169	151	2	2	0	0	0	0	0	0	0	0	0	0	1589
CLG In P	784	658	32	34	0	0	0	0	10	7	0	0	4	3	0	1	1533
CLP In P	1395	1203	96	97	0	0	1	4	16	5	0	1	1	1	0	0	2820
CLF In P^{F}	1927	1571	58	32	0	0	1	0	7	4	0	0	0	1	0	0	3601

TABLE 5—*Tests of CIII × ru hy th st cu sr e^s ca*

C III	Non-crossovers		4		5		7		4, 5		4, 7		Total
CLG In P	544	311	41	39	13	11	10	2	0	1	2	0	974
CLF In P^F	986	540	7	10	2	2	2	1	0	0	0	0	1550

TABLE 6—*Tests of CIII × ru hy st p^p ss e^s*

C III	Non-crossovers		3		4		3, 4		Total
CLF In P	1727	1222	72	66	65	63	6	0	3221
CLP In P	432	339	1	6	5	5	0	0	788
CLF In P^F	590	443	5	9	6	9	0	1	1063
CLo In P^o	280	237	11	9	9	7	1	0	554

TABLE 7—*Tests of H against st sbd In P^{sbd} ro ca*

Sequence of loci	0		1		3		4		1, 3		1, 4		Total
st sbd H ro ca	7700	2908	276	663	3	0	29	10	2	1	6	7	11605

TABLE 8—*Tests of inversion × ru st p^p ss e^s*

Inversion	Non-crossovers		1		2		3		1, 2		1, 3		2, 3		1, 2, 3		Total
In E^{Pr}	42	36	43	25	5	0	1	1	2	1	1	0	0	0	0	0	157
In Mo	487	367	306	327	20	15	3	2	9	10	1	0	0	1	0	0	1548
In Mo^B	156	117	92	112	6	4	0	1	2	2	0	0	1	0	0	0	493
In Mo^{NO}	266	198	165	142	10	7	4	7	3	4	0	1	0	0	0	0	807
In P^{Ci}	100	76	67	85	17	20	1	2	14	12	3	0	1	0	0	0	398
In P^{En}	381	264	249	274	18	12	1	0	10	9	0	1	0	0	0	0	1219
In P^G	52	37	31	25	3	1	0	0	1	0	0	0	0	0	0	0	150
In P^W	342	277	253	285	28	23	3	4	12	10	0	0	0	0	0	1	1238

TABLE 9—*Tests of inversion × st sr e^s ro ca*

Inversion	Non-crossovers		1		2		3		4		1, 4		2, 4		Total
In E (beaded)	187	179	32	30	0	0	0	0	0	0	0	0	0	0	428
In E (ebony)	502	445	18	27	1	0	0	0	0	0	0	0	0	0	993
In E (eosin)	800	753	110	79	0	1	0	0	0	0	0	0	0	0	1743
In E^{Pr}	2344	2182	247	260	3	5	0	1	0	0	0	0	1	0	5043
In Mo	855	803	77	79	0	1	0	0	0	0	0	0	0	0	1815
In Mo^B	607	562	66	55	0	0	0	0	0	0	0	0	0	0	1290
In P	470	483	35	44	0	0	0	0	1	1	0	0	0	0	1034
In P^{Ci}	599	531	67	56	0	0	0	0	2	2	0	0	0	0	1257
In P^{En}	828	832	53	63	0	0	0	1	0	3	0	0	0	0	1780
In P^G	692	651	58	65	0	0	0	0	1	1	0	0	0	0	1468
In P^o	723	742	64	70	0	0	0	1	3	4	0	1	0	0	1608
In P^{sbd}	504	447	21	34	0	0	0	0	1	1	0	0	0	0	1008
In P^W	330	302	37	33	0	0	0	0	2	5	1	0	0	0	710

TABLE 10—*Tests of heterozygous In Mo*

Loci	Experiment	0	1	2	3	1, 2	Total
D st Sb sr.....	D st sr × Sb	439 480	27 19	73 71	1 2	1 1	1114
	D Sb × st sr	680 680	15 17	40 53	0 0	1 0	1486

TABLE 11—*Tests of st In against CIIIL sr e^s ro ca*

C III's	Loci	0	1	2	1, 2	Total
CLF/InE.....	st sr e^s ro ca	558 553	83 65	2 0	0 0	1261
CLP/InMo.....	st sr e^s ro ca	608 576	92 89	2 3	0 1	1371

TABLE 12—*Tests of inversion × th cu sr e^s ro ca*

Inversion	Non-crossovers	1	2	3	1,2	Total
In E^{Pr}.....	1563 1113	168 183	65 74	2 0	6 7	3181
In Mo^{NO}.....	395 278	26 59	16 16	0 1	3 0	794

C III R's produce any effect at all to the left of pink; all of them definitely reduce pink spineless, and very greatly reduce the spineless-ebony-rough-claret values. Stripe ebony becomes zero in the In P series, but is about 0.1 in the other two. Ebony rough and rough claret are zero in the Mo series; in the E series they are nearly so, and the few crossovers observed have been doubles. In the P series ebony rough is less than 0.1, and rough claret averages about 0.4; these are mostly single crossovers, not to be compared with those occurring in the same intervals in the presence of the E series. These results may be diagrammed as here shown.

	sr e	e ro	ro ca
Standard.....	8.7	20.3	9.6
E.....	0.1	0	0
Mo.....	0.1	0	0
P.....	0	0.0+	0.4

LOCI OF C III R'S

Single crossovers produced in experiments with C's (and double crossovers in which both crossovers are outside the region of maximum effect) have been tested to determine the loci of the C's. Such tests have shown that In E lies to the right of pink and In E^{Pr} to the right of stripe. In Mo and In Mo^{NO} lie to the right of stripe and In Mo^{B} to the right of scarlet. There can be no doubt that all the members of both the E and Mo series lie to the right of stripe. There is no single crossing over to the right of the stripe-ebony interval in these cases, so that the method is not available for determining the right-most limit of the inversion, which in fact is, for In E at least, probably the right end of the chromosome itself. In the case of the In P series, In P, In P^{Ci}, In P^{En}, In P^{F}, In P^{o}, and InP^{W}, all lie to the right of scarlet; In P^{sbd} to the

right of stubble;[1] In P^{sbd} and In P^{W} to the left of claret, and In P, In P^{o}, and In P^{En} to the left of rough. It may be assumed that all the members of this series lie between stubble and rough.

It will be observed that this result places each of the C's itself in the region in which crossing over is most markedly reduced—a result observed also in the case of C's in regions other than the right limb of chromosome III. These results also place limits on the possible lengths of the inverted sections, which will be discussed later in connection with the data from homozygous C's.

EFFECTS OF C III R'S WHEN HOMOZYGOUS

Muller (1916) showed that homozygous In E gives free crossing over, and I showed (Sturtevant, 1917) the same thing for C II R N. As will appear below, the same result obtains in the cases of In E^{Pr}, In Mo, In P^{o}, and In P^{sbd}, as also of C II L Cy and C II R Cy. These data will be presented and discussed below; the point here is simply that such free crossing over has been obtained in every case in which a given C of the present type has been studied in homozygous form. This fact has led to a systematic testing of different C's against each other, the assumption being that like ones would give free crossing over when placed in the same fly; unlike ones would not. Such has proven to be the case, there being no combinations that have given results unexpected on this assumption. C's that satisfy this test of likeness, but are different in origin, are here referred to as "allelomorphic," though in the case of inversions it must be admitted that the term is perhaps not strictly correct. Nevertheless its use seems justified as a matter of convenience.

TESTS OF CIII R'S AGAINST EACH OTHER

Tables 13 to 16 show the data obtained from females carrying a $C_{III\ R}$ in each chromosome (*i. e.*, homozygous for any one or heterozygous for any two simultaneously). This unwieldy mass of raw data has been summarized in two separate ways in tables 17 and 18.

TABLE 13—*Tests of $C_{III\,R}$'s against each other. Two-point experiments*

Experiment number	C's	Loci	Cross	Non-crossovers		Cross-overs		Total
1.....	E/E	st e	st e × +	109	94	89	70	362
5.....	E/Mo^{B}	st e	e × st	329	317	4	12	662
8.....	E/P^{Er}	st e	e × st	127	117	5	6	255
10.....	E/P^{sbd}	D sbd	+ × D sbd	189	257	24	12	482
20.....	E^{Pr}/P^{W}	st ca	+ × st ca	166	165	8	6	345
29.....	Mo/P^{M}	st sr	+ × st sr	107	59	0	0	166
34.....	Mo^{B}/P^{o}	st ca	+ × st ca	210	212	7	3	432
36.....	C_{LP} P/P^{o}	st ca	+ × st ca	117	102	111	89	419
40.....	C_{LP} P/P^{W}	st ca	+ × st ca	191	194	157	155	697
44.....	C_{LF} P^{F}/P^{W}	st ca	+ × st ca	119	107	100	92	418
47.....	P^{o}/P^{o}	st ca	+ × st ca	62	48	44	34	188
50.....	P^{o}/P^{W}	st ca	+ × st ca	163	127	132	127	549
51.....	P^{sbd}/P^{sbd}	st ca	+ × ts ca	131	149	115	128	523

[1] Crossing over between In P^{sbd} and stubbloid, the recessive allelomorph of stubble with which it was associated when first found, has not been observed in diploid females. One such crossover was obtained from a triploid female, and from this single fly was produced a stock of stubbloid free from C III. This stock has been crossed to stubble, and tests of the resulting stubble-stubbloid heterozygotes have shown that there is no crossing over between the two genes. This fact, together with the fact that such heterozygotes show the stubble character in more extreme form than either heterozygous stubble or homozygous stubbloid, is the basis for treating the two genes as allelomorphic. A detailed study of the somatic effects of these genes is being carried out by Professor T. Dobzhansky.

TABLE 14—*Tests of $C_{III\ R's}$ against each other. Three-point experiments*

Experiment number	C's	Loci	Cross	Non-crossovers		Single crossovers				Double crossovers		Total
						region 1		region 2				
7	E/P^{Ci}	h st e	e × h st	136	118	47	54	10	16	8	4	393
9	E/P^{o}	st e ca	e × st ca	241	180	6	0	0	0	0	0	427
11	E/P^{sbd}	st sbd ca	+ × st sbd ca	324	335	13	16	0	0	0	0	688
12	E/P^{sbd}	st e ca	e × st ca	142	120	4	5	0	0	0	0	271
13	E/P^{W}	h st e	e × h st	181	167	61	67	5	8	1	2	492
17	E^{Pr}/Mo^{NO}	st cu e	e^{12} × st cu	89	78	2	13	6	3	0	0	191
23	C_{LP} Mo/Mo^{B}	st Sb sr	Sb sr × st	110	102	13	22	6	4	0	0	257
26	Mo/C_{LP} P	st Sb sr	+ × st Sb sr	756	771	8	6	0	0	0	0	1541
27	Mo/P^{En}	st Sb sr	+ × st Sb sr	509	467	18	28	0	0	0	0	1022
28	Mo/C_{LF} P^{F}	st Sb sr	+ × st Sb sr	167	161	3	7	0	0	0	0	338
31	Mo/P^{sbd}	st sr ca	sr × st ca	426	428	34	33	0	0	0	0	921
32	Mo/P^{sbd}	st sbd ca	+ × st sbd ca	479	325	58	69	0	0	0	0	931
33	Mo/P^{W}	st sr ca	sr × st ca	225	266	8	13	0	0	0	0	512
37	C_{LP} P/P^{sbd}	st sbd ca	+ × st sbd ca	134	96	33	33	107	85	19	18	525
41	P^{Ci}/P^{sbd}	st sbd ca	+ × st sbd ca	126	71	36	29	78	86	27	15	468
42	P^{En}/P^{sbd}	st sbd ca	+ × st sbd ca	181	136	52	44	120	109	34	30	706
46	$C_{LM}P^{M}$/P^{o}	D st ca	+ × D st ca	127	167	0	0	107	105	1	0	507
49	P^{o}/P^{sbd}	sbd cd^2 ro	cd^2 × sbd ro	3594	2895	379	350	1182	1029	44	22	9495
52	P^{sbd}/P^{W}	st sbd ca	sbd × st ca	119	135	20	37	93	127	24	13	568

TABLE 15—*Tests of $C_{III\ R's}$ against each other. Four-point experiments*

Experiment number	C's	Loci	Cross	Non-crossovers		Single crossovers						Multiple crossovers								Total
						1		2		3		1, 2		1, 3		2, 3		1, 2, 3		
2	E/E^{Pr}	st sr ro e	+ × st sr ro e^{s}	212	185	68	73	124	128	92	81	13	26	34	37	31	15	9	4	1132
3	E/E^{Pr}	st sr ro e	e × st sr ro	148	158	34	45	79	69	44	41	5	2	9	6	3	7	0	0	650
4	E/Mo	D st sr e	D st sr × e	308	337	7	10	20	26	0	0	0	0	0	0	0	0	0	0	708
6	E/P	st e ro ca	e × st ro ca	199	215	25	17	0	0	0	0	0	0	0	0	0	0	0	0	456
14	E^{Pr}/E^{Pr}	st sr ro e	ro e^{s} × st sr	117	125	44	42	66	66	24	24	14	18	12	14	13	4	0	2	585
15	E^{Pr}/E^{Pr}	Sb sr ro e	Sb ro e × sr	156	148	6	7	98	76	49	53	0	4	3	3	15	25	0	0	643
18	E^{Pr}/P^{Ci}	st sr e ro	sr e^{s}ro × st	283	301	65	55	0	0	0	0	0	0	0	0	0	0	0	0	704
21	Mo/Mo	D st Sb sr	D Sb sr × st	336	335	16	14	80	73	12	16	5	6	0	1	1	3	0	0	898
22	Mo/Mo^{B}	D st Sb sr	D Sb sr × st	227	221	1	6	34	19	9	5	0	1	0	0	0	0	0	0	523
24	Mo/Mo^{NO}	st Sb sr e	E^{12} × st Sb sr	118	134	20	18	2	4	27	28	0	0	1	1	0	0	0	0	353
25	Mo/Mo^{NO}	st Sb sr e	+ × st Sb sr e^{12}	247	203	84	49	11	12	18	23	1	1	7	2	0	0	0	0	658
30	Mo/P^{o}	D st sr ca	ca × D st sr	343	285	8	13	27	18	0	0	1	1	0	0	0	0	0	0	696
35	Mo^{NO}/P^{sbd}	st sbd ro ca	+ × st sbd ro ca	229	68	7	17	0	0	0	0	0	0	0	0	0	0	0	0	321
38	C_{FL} P/P^{sbd}	st sbd ro ca	+ × st sbd ro ca	96	63	45	37	80	55	23	16	16	17	8	16	14	9	6	6	507
39	C_{PL} P/P^{sbd}	st sbd ro ca	+ × st sbd ro ca	141	89	57	55	105	69	42	21	34	32	13	18	21	9	7	5	718
43	$C_{FL}P^{F}$/P^{sbd}	st sbd ro ca	+ × st sbd ro ca	402	199	51	88	151	181	79	27	19	23	9	10	8	12	2	0	1261
45	P^{G}/P^{sbd}	st sbd ro ca	+ × st sbd ro ca	159	94	26	26	72	70	27	11	7	2	1	5	5	2	0	0	507
48	P^{o}/P^{sbd}	D st sbd ca	D st ca × sbd	116	86	1	1	15	25	75	70	1	1	3	0	5	12	0	0	411

of the four types. In Mo and In P^{sbd} were each tested against all but two of the reducers. It seems clear that the evidence is adequate to make the classification valid.

In table 18 are shown the average crossover percentages for a few selected intervals. The values for heterozygous C's (from table 3) are added for comparison. In this table all allelomorphic C's are totaled as identical, though the raw data indicate that (at least in the P series) this is not strictly true. This point will be discussed below; but it is sufficient to necessitate caution in drawing conclusions from the table, especially since here, as in table 3, there are minor variations that make detailed comparisons difficult.

TABLE 18—*Summary of crossover values given by various combinations of* $C_{III'R_S}$

	st sr	Sb sr	Sb cd	Sb ro	sr e	sr ro	e ro	cd ro	ro ca
+ /+.....	16.5	3.8	17.4	31.4	8.7	27.6	20.3	15.4	9 6
+ /E.....	10.4	..	..	..	0.1	0.1	0.+	..	0.+
+ /Mo.....	12.3	0.1	..	..	0.1	0.2	0	..	0
+ /P.....	6.0	..	..	0.+	0	0.+	0.1	..	0.5
E /E.....	21.6	3.6	..	36.3	43.7	29.3	21.7	..	..
E /Mo.....	13.7	1.4	..	1.9	0.2	0.5	0	..	..
E /P.....	14.5	..	..	..	0	0	0	..	0
Mo/Mo.....	19.3	3.3	..	..	10.6	..	..	..	..
Mo/P.....	3.9	0	..	0	..	..	..	..	0
P /P.....	..	..	8.4	32.1	..	..	..	24.0	14.5

The table indicates that females heterozygous for two C's of different types show a summation of the suppression effects characteristic of each C. The most exceptional value shown, from this point of view, is the st sr value of 14.5 given by E/P, which would be expected to be nearer the 6.0 shown by +/P. Other similar exceptions can be found in the raw data. They have not been satisfactorily explained, but are probably due to unanalyzed minor crossover modifiers, which are known to exist in this region.

The most interesting rows of table 18 are those concerning homozygous E, Mo and P. These may be considered in turn, but in reverse order.

In P was shown above to lie between sb and ro, where its maximum (heterozygous) effect occurs. The only locus within this region that has been obtained in mutant form in an In P chromosome is cardinal, studied by Mr. S. Shlaer. As the tables show, Mr. Shlaer's extensive data give—

Sb cd = 8.4, cd ro = 24.0 — total = 32.4. Standard is
Sb cd = 17.4, cd ro = 15.4 — total = 32.8.

The conclusion seems justified that cardinal has been moved 9 units to the left of its normal position in the In P chromosome. In other words: In P consists of an inverted section between Sb and ro including cd, and which can be shown to be not less than 9 units nor more than 25.8 units long.

In Mo lies to the right of sr, and wholly prevents crossing over in the e-ca region when it is heterozygous. Only one mutant gene lying in this region has been studied in homozygous Mo—namely e. The table shows that sr e is 10.6, standard being 8.7. The change here is slight, and reference to the raw data (experiments 24 and 25) shows that the two experiments did not

give consistent results. One gave 57/363 = 16.1, the other gave 50/568 = 7.6. Pending further experiments, these data are not adequate for analysis. It may be noted, however, that Sb sr gives 3.3, in excellent agreement with the standard 3.8 and definitely different from the +/Mo value of 0.1. It is this value that serves to identify the type of In Mo^{B}, which was discarded before ebony-12 was discovered in In Mo^{No}—that discovery having first made possible the testing of the ebony locus in homozygous In Mo.

Homozygous In E has been discussed previously (Sturtevant, 1926). The data show the sequence of genes to be sr-ro-e, instead of the standard sr-e-ro.[1] A comparison of the two maps follows.

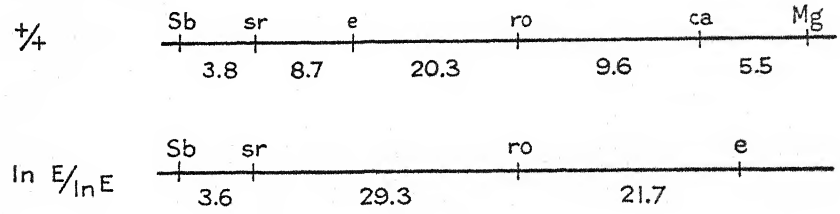

FIG. 1

The two comparable intervals, Sb sr and e ro, are nearly the same in the two cases (3.8 and 3.6, 20.3 and 21.7). This result, together with the agreement in the Sb-ro value for homozygous In P, suggests that amounts of crossing over are independent of the position of sections in the chromosomes: that, given a like sequence of genes in the two chromosomes, and like environmental conditions (age, sex, temperature), the amount of crossing over in a given section is a function of the nature of the section itself. If this conclusion be adopted in the present case (though admittedly it needs more extensive testing on other inversions), a further corollary follows from it. According to the standard map there are 15.1 units known to the right of rough (this being the map distance to Minute-g, the rightmost known locus). The map for homozygous In E shows 29.3 units between stripe and rough, with the probability that the interval is long enough to have some undetectable double-crossing over within it. Not more than 8.7 units of these 29.3 can represent uninverted chromosomes, this being the standard sr e distance. One may suspect that about 5.5 units (29.3−15.1−8.7) at the right end of chromosome III (standard map) remain to be discovered—these units lying between sr and ro in the In E/In E map. The left end of the inverted section is known to lie between sr and e (standard map); no matter how many units it lies to the left of e, those units are to the right of e in the In E/In E map, and hence can not be detected there. Thus 5.5 units is the minimum value to be added to the standard map, while the maximum is 5 5 plus 8.7 = 14.2. However, these speculations must not be taken too seriously, since they are based only on the crossover values shown by the total data for homozygous In E. Examination of experiments 2, 3, 14 and 15 shows that the sr ro value varies from 25.4 to 33.9 and ro e from 15.9 to 26.9 in separate crosses.

[1] Dr. J. Schultz has unpublished data on the behavior of cardinal in homozygous In E. As expected, these data show that cd lies a few units to the left of e, instead of a few units to the right of it as in the standard map.

CROSSING OVER IN FEMALES HETEROZYGOUS FOR INVERSIONS

Females heterozygous for inversions give very few crossovers in the region concerned, but the few that are produced are of considerable theoretical interest and are at times useful in that some of them carry mutant genes introduced into the inversion. Those occurring in the case of heterozygous In E^{Pr} have already been discussed (Sturtevant, 1926), and may be most conveniently used here as examples.

Table 9 shows that, from In E^{Pr}/st sr e^s ro ca, 5043 flies were obtained, of which only two represented crossing over to the right of e^s. These were: one st sr e^s and one e^s ro. Both crossover chromosomes were tested; the first was found not to carry the inversion, while the second did carry it and was also shown not to be lethal. Owing to its non-lethal nature, the inversion with e^s and ro introduced must be supposed to form part of a chromosome that carries substantially the normal complement of genes.

Analysis of these two crossovers indicates that conjugation must occasionally occur in such fashion that like genes come to lie opposite each other in the inverted sections, as shown in figure 2, where $+^1$ and $+^2$ represent the two ends of the inverted section.

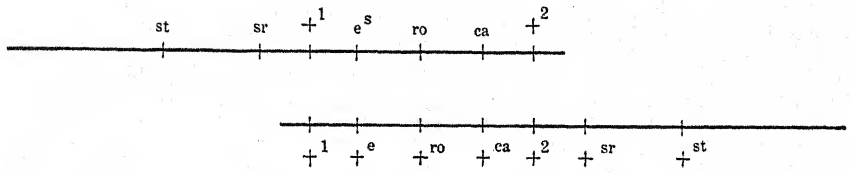

FIG. 2

The two crossovers observed were both doubles; the st sr e^s between e^s and ro and between ca and $+^2$, the e^s ro between $+^1$ and e^s and between ro and ca. It will be seen that all single crossovers receive the left end of the chromosome in duplicate or not at all; zygotes receiving such chromosomes would not be expected to be viable, and the results show that they are in fact not viable. It may be noted further that such crossover chromosomes always have either two spindle-fiber attachments or none,[1] so that perhaps the chromosomes are not capable of reproducing themselves.

Claret has been represented as lying in the inverted section, because only in this way can the st sr e^s crossover be interpreted; if the right end of the inversion lies between rough and claret a st sr e^s crossover will necessarily also be ca.

In the region to the right of sr, two normal chromosomes (*i. e.*, without inversions) give between 2 and 3 per cent of double crossovers. Heterozygous In E^{Pr} gave $\frac{2}{5043} = 0.04$ per cent. One may conclude that the type of reversed conjugation shown in figure 2 occurs in not more than about 2 per cent (100:2 = X: 0.04, hence X = 2) of the eggs concerned.

One of the crossovers in the presence of heterozygous In E described by Muller (1918) turns out, on analysis, to have been a double within the

[1] The spindle-fiber is attached between st and sr, very close to the locus of p^p.

inverted section and at the same time a crossover to the left of it. Evidently the two long ends shown in the figure may bend around and conjugate with each other.

Similar double crossovers are discussed in this paper in connection with $C_{III\ L\ P}$, $C_{III\ L\ G}$, and $C_{II\ L\ Cy}$.

$C_{III\ L's}$

The C's affecting the left limb of chromosome III have not been worked with very extensively. No mutant gene (in the affected region) with a known locus on the standard map has yet been obtained in a $C_{III\ L}$, and their relation to each other is therefore not known. A list of those that have been found follows.

$C_{III\ L\ P}$—Payne (1924) found this present in some, but not all, of the third chromosomes of a stock from Bloomington, Indiana.

$C_{III\ L^o}$—Bridges found this to be present in the left limb of the original In P^o chromosome, which came from mutant stocks of unknown wild origin.

$C_{III\ L\ M}$—Mrs. Morgan found this, also in a mutant stock and in the chromosome whose right limb carried In P^M.

$C_{III\ L\ G}$—This was found in the wild stock from Georgetown. Texas, in which In P^G occurred. The original $C_{III\ L\ G}$ chromosome itself carried no $C_{III\ R}$; in addition one chromosome III from this stock carried no C at all.

$C_{III\ L\ F}$—Mr. H. D. Fish discovered this, associated with In P^F, in a wild stock from Olympia, Washington. This wild stock also contained third chromosomes that had no C's.

It will be observed that all five of these $C_{III\ L's}$ were found in stocks that also carried In P's, which were in the same chromosomes in four cases but not in the Georgetown stock. This point will be discussed again, after the data on chromosome II have been presented.

Tables 4, 5, 6 and 11 show the data obtained from females carrying both $C_{III\ L's}$ and $C_{III\ R's}$. In addition several thousand flies have been reared from females carrying these $C_{III\ L's}$ but no $C_{III\ R's}$. These data show that st p is reduced to about 0.3 (6 crossovers in 2267 flies, when no $C_{III\ R}$ is present); ru h and h st are both 0. The only exception to the last values is the ru st sr e^s ro ca crossover from $C_{L\ G}$ In P/ru h st sr e^s ro ca, that is recorded in table 4. This fly, a ru-h, h-st, e^s-ro triple crossover, was tested. The test showed that it was correctly classified and also that it carried no C_{III}. This result is consistent with the view that $C_{L\ G}$ is an inverted section including the h locus—but more evidence is needed before this conclusion can be finally accepted.

Payne (1924) recorded several crossovers between ru and st in females heterozygous for $C_{L\ P}$. Among nearly 30,000 flies there were 3 ru-h crossovers, 3 h-st, and one ru-h h-st double crossover. Apparently none of these flies were tested, so that the result can not be further analyzed. However, the simplest interpretation of the data, as they stand, is that $C_{III\ L\ P}$ is an inversion that includes h, but not ru or st.

Tests of crossovers have shown that $C_{L\ F}$ lies to the left of sr, $C_{L\ P}$ and $C_{L\ G}$ to the left of ss, and C_{L^o} to the left of p. Evidently all four lie in the region of maximum effect, *i. e.*, in the left limb of chromosome III, within which they all suppress practically all crossing over.

$C_{II\ L\ N}$ AND $C_{II\ R\ N}$

I have already described (Sturtevant, 1917, 1919) the two $C_{II's}$ found in a stock collected at Liverpool, Nova Scotia, in 1913. The linkage data may be summarized as in table 25 of the 1919 paper (table 19).

TABLE 19—*$C_{II\ N}$ combinations*

Loci	+/+	C_LC_R/+	C_L/+	C_R/+	C_L/C_R	$C_L C_R/C_R$	C_R/C_R
S b	37.9	0	0	42.4	0	0.3*	38.2
b pr	6.2	0.2	0.5	6.2	0.2	0.1	3.5
b vg	17.8	1.2	13.4	8.9	..	..	..
pr c	19.9	1.1	20.5	1.6	2.9	..	..
pr sp	46.5	1.1	47.4	2.9	3.6	47.4	41.5
c sp	30.2	0.1	35.3	0.1	0.1	..	..

* Probably really 0. The recorded crossovers not tested and probably due to errors in classifying Star.

$C_{II\ L\ N}$ lies to the left of purple; in heterozygous form it inhibits all S b crossing over and greatly reduces b pr. It has not been possible to study this reducer in homozygous form, and no allelomorphs have been found.

$C_{II\ R\ N}$ lies between purple and plexus. In heterozygous form it reduces the pr c and c sp intervals greatly; in homozygous form it does not influence the pr sp separation-frequency, but no intermediate loci have hitherto been recorded in experiments with homozygous $C_{II\ R\ N}$.

Three new allelomorphs of $C_{II\ R\ N}$ have been found, and px has been put into the original $C_{II\ R\ N}$ chromosome by crossing over. Accordingly the case can now be described in somewhat more detail. The new allelomorphs are all from wild stocks of southern origin, as follows:

$C_{II\ R\ N\ CU}$—found (1926) in the Cienfuegos, Cuba, stock that also carried In P^{ci}.

$C_{II\ R\ N\ K}$—found in a wild stock collected in 1924 at Kushla, Alabama.

$C_{II\ R\ N\ LA}$—found in wild stock collected in 1926 by Dr. C. I. Bliss at New Orleans, Louisiana.

The results given by these three in heterozygous form are shown in table 20.

TABLE 20—*$C_{II\ RN}$/b pr c sp*

	0		1		2		1.2		Total
$C_{II\ R\ N\ CU}$	304	296	19	9	5	6	0	0	639
$C_{II\ R\ N\ K}$	445	347	28	38	6	7	0	1	872
$C_{II\ R\ N\ LA}$	233	232	5	10	6	0	0	0	486

So far as these data show, b pr crossing over is somewhat reduced, pr c markedly so and c sp entirely suppressed—results perhaps significantly more extreme than those due to $C_{II\ R\ N}$ itself. Since the test stocks were different and the technique several years later than the $C_{II\ R\ N}$ experiments, these differences need not be insisted on too strongly.

$C_{R\ N\ CU}$ and $C_{R\ N\ LA}$ were obtained with dp, and were crossed to $C_{II\ L\ N}$ $C_{II\ R\ N}$ px sp. The resulting F_1 females gave, respectively, dp px: $\frac{269}{665} = 40.5$ and 59/154 = 38.3; px sp: 30/665 = 4.5 and 9/154 = 5.3. $C_{R\ N\ K}$ was crossed to $C_{II\ L}\ C_{y\ pr}\ C_{II\ R\ N\ sp}$, giving (on backcrossing) Cy pr, 1/704 = 0.1; pr sp, 316/704 = 44.9.

From these data the allelomorphism of all three to $C_{II\ R\ N}$ is clear. It is also evident that, in homozygous $C_{II\ R\ N}$, pr px = 40± and px sp = 5±. The "standard" value for px sp is 6.5, and we have already seen that pr sp gives close to the standard separation-frequency. That is, homozygous $C_{II\ R\ N}$ gives standard values for b, pr, px and sp. The presumption is that $C_{II\ R\ N}$ is an inversion lying between pr and px, but this conclusion can not yet be taken as established.

$C_{II\ L\ Cy}$ AND $C_{II\ R\ Cy}$

Ward (1923) described the dominant second chromosome mutant curly and the $C_{II\ L}$ and $C_{II\ R}$ associated with it. The $C_{II\ L}$ almost completely prevents crossing over between S and b; the $C_{II\ R}$ greatly reduces pr sp, being itself not separable from the L-c region, where its maximum effect is evident.

I have obtained two crossovers in the S b region; one of these was a Cy b, that carried the $C_{II\ L}$ and made it possible to deal with the black locus in homozygous $C_{II\ L}$; the other was a dp from S dp b $C_{II\ L}$ Cy/+. This last specimen was tested and was found not to carry the $C_{II\ L}$—a result strongly suggesting that $C_{II\ L\ Cy}$ is an inversion that includes the dp locus.

Both the Star and the dumpy in the Cy chromosome just mentioned arose by mutation (Star found by Dr. Helen Redfield, dumpy by Dr. H. J. Muller). They, with the black obtained by crossing over, have been used in studying homozygous $C_{II\ L\ Cy}$. Most curly chromosomes now carry lethals, but crosses of remotely related strains often yield some homozygous curly flies, which are then moderately fertile.

S dp has not been tested directly in females homozygous for $C_{II\ L\ Cy}$, but from results obtained in dealing with $C_{II\ L\ T}$ (see below) it may be inferred that it gives a value of about 30. Direct tests of dp b give $\frac{75}{461} = 16.3$ per cent. The resulting S-b distance of about 46 is in good agreement with the standard value of 46.5; but dp is, on the standard map, about 11 units from S and 35.5 from b. That is to say: the inference from the double crossover obtained from heterozygous $C_{II\ L\ Cy}$ is verified; $C_{II\ L\ Cy}$ is an inversion, including the dp locus but not S or b. The crossover values for homozygous $C_{II\ L\ Cy}$ are not determined accurately enough to warrant any more detailed analysis of the possible extent of the inversion.

A test of $C_{II\ L\ Cy}$ $C_{II\ R\ Cy}/C_{II\ L\ N}$ $C_{II\ R\ N}$ gave no crossovers (among 297 flies) for the loci S, dp, Cy, px and sp. It follows that both the $C_{II\ L's}$ and $C_{II\ R's}$ are distinct.

Another $C_{II\ L}$, known as $C_{II\ L\ T}$, was found in the "three-ple" mutant stock (ru hy st p^p ss e^s). In heterozygous females this gave S-b-pr = 0 (589 flies), and dp-b-pr = 0 (884 flies). It is, then, like $C_{II\ L\ Cy}$ and $C_{II\ L\ N}$, a suppressor of crossing over throughout the left limb of chromosome II. $C_{IIL\ Cy}/C_{II\ L\ T}$ gave the sequence S dp Cy b. The crossover values were S dp. 91/625 = 14.6

per cent; dp Cy, 112/2745 = 4.1 per cent; Cy b, 25/2120 = 1.2 per cent. That is to say: dp b = 4.1 + 1.2 = 5.3, as opposed to the 16.3 found in homozygous $C_{II\ L\ Cy}$.

Numerous tests have been carried out in an attempt to analyze the difference between $C_{II\ L\ T}$ and $C_{II\ L\ Cy}$. Both carried lethals when the experiment was begun, and this resulted in failure to obtain many of the combinations of crossover chromosomes with each other and with the original $C_{II\ L\ Cy}$ or $C_{II\ L\ T}$ chromosomes. Of the combinations obtained, only a few were heterozygous for all the mutant loci concerned. For these reasons the analysis has not yet been completed; but one result is perhaps worth recording. A chromosome carrying S, and the left portion of $C_{II\ L\ Cy}$ with the right portion of $C_{II\ L\ T}$, has given (against an unmodified $C_{II\ L\ Cy}$ chromosome) a S dp value of approximately 30 in several cultures. This is the basis for the value of 30 tentatively assigned, above, to the S dp interval in homozygous $C_{II\ L\ Cy}$. It should be added that this value was apparently associated with the low value for dp b that characterizes $C_{II\ L\ Cy}/C_{II\ L\ T}$, not with the higher value that is shown by homozygous $C_{II\ L\ Cy}$.

The relation of $C_{II\ L\ Cy}$ and $C_{II\ L\ T}$ is, so far, unique among crossover reducers, though some of the In P allelomorphs perhaps show the same relation to a very much smaller degree. Its final solution should throw light on the whole question of inversions.

CROSSOVER MODIFIERS IN THE X-CHROMOSOME

The twelve wild stocks recorded in table 1 as tested for variations in linkage in chromosome I did not yield any striking modifiers; and there are no recorded cases in the literature that can be simply interpreted as inversions in the X. There are, however, several recorded crossover modifiers, that may be briefly described.

Detlefsen (1920), Detlefsen and Roberts (1921), and Detlefsen and Clemente (1923) selected for decreased crossing over in several lines, and obtained positive results. The data do not give any clue as to the genetic basis of these variations, except in the case of one line. In this case the major effect seems to have been due to a sex-linked gene (or chromosome aberration) that was effective when heterozygous. The reduction was most marked at the left end of the chromosome, and became progressively less toward the right end. The data were not presented in such fashion that the frequency of double crossing over can be determined, and no tests of crossovers were recorded. It is not known how the reducer acted when homozygous.

Mrs. Morgan (1926) has reported briefly a dominant modification that suppresses nearly all crossing over in the X, an unusually high percentage of the crossovers that do occur being doubles. These relations strongly suggest an inversion; but cytological examination has shown that the chromosome concerned is doubled on itself in the form of "an almost or entirely closed and somewhat rounded letter U" in oogonial metaphases. It seems likely that this abnormal shape (perhaps correlated with an unusual type of spindle-fiber attachment) is the basis of the reduction in crossing over. Muller has briefly referred to a similar case, that is still unpublished.

Anderson (in press) and I (unpublished) have studied dominant crossover reducers located near vermilion that greatly increased the frequency of

non-disjunction. These may represent inversions; but in each case it was possible to show that the inversion, if present, must be very short. Neither of these cases could be studied in homozygous flies.

INVERSION IN SIMULANS AS COMPARED TO MELANOGASTER

The first demonstrated case of inversion was that which characterizes the third chromosome of *Drosophila simulans* as compared to that of *melanogaster* (Sturtevant and Plunkett, 1926). The two chromosomes may be represented as shown in the diagram.

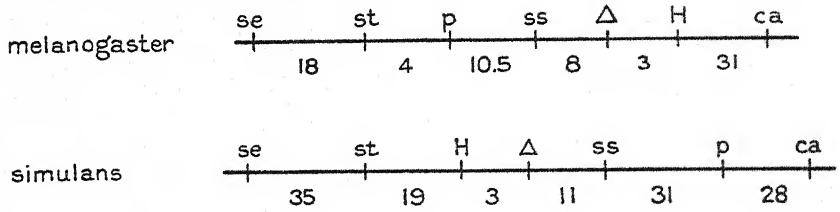

FIG. 3

That is, a section including p, ss, Δ, and H has been inverted. The left end of this section must lie close to the point of spindle-fiber attachment; the right end is evidently beyond the H locus of *melanogaster*, since st H in *simulans* is 15 units greater than st p in *melanogaster*. It is, however, difficult to make any detailed analysis, since the *simulans* map shows larger values than that of *melanogaster* in nearly all the comparable intervals, including se st which is wholly outside the inverted section. The whole chromosome (including all known loci, many of which are known in only one species) is 106 units long in *melanogaster* and 134 in *simulans*, with the probability that *simulans* will be increased relatively more by the discovery of new mutant genes.

Tests of various wild stocks of *simulans* (from Massachusetts, New Jersey, Minnesota, Florida, Alabama, Louisiana and California) have all given the same sequence of third chromosome loci, showing that the inversion is really characteristic of the species. It should be noted that it is different from all three types of $C_{III\ R}$ known in *melanogaster*, in that none of these extend far enough to the left to include p.

Tests of wild stocks and routine experiments have failed to show any powerful C_I or C_{III} in *simulans;* a single $C_{II\ L}$ was found in a wild stock collected by Dr. C. I. Bliss at New Orleans, Louisiana, in 1926. This may represent an inversion; but the mutant genes in the left limb of chromosome II are so unsatisfactory that it has not been possible to make any detailed study of the case.

TESTS FOR IDENTITY OF IN P ALLELOMORPHS

The various In P allelomorphs do not all give the same results, either against normal chromosomes or in combinations with each other. It is probable that these differences are of the same nature as the unanalyzed variations recorded for the right limb of chromosome III by Bridges and Morgan (1923). However, it seemed possible that some of these allelomorphs might represent inversions of sections differing slightly in length, and two tests have been carried out to

check this hypothesis. Both tests gave negative results, but they may be briefly described here.

If we suppose the normal sequence of genes to be A B C D E F, one inversion to be A E D C B F, and the other A B E D C F, then in the heterozygote $\frac{\text{A E D C B F}}{\text{A B E D C F}}$, single crossing over between D and C will give A E D C F and A B E D C B F. One of these carries no B, the other carries two B's. If we suppose the inversion to differ at both ends, $\frac{\text{A E D C B F}}{\text{A B D C E F}}$ gives A E D C E F (no B, 2 E's) and A B D C B F (no E, 2 B's). One other possible type, $\frac{\text{A B E D C F}}{\text{A D C B E F}}$, gives A B E D C B E F (2 B's, 2 E's) and A D C F (no B, no E). In each case at least one of the two kinds of chromosomes resulting from single crossing over is deficient for at least one gene. This relation is the basis of the two tests that were made.

From In P^F/sbd In P^{sbd} ro, each non-crossover chromosome was shown to be free of recessive lethals, and three ro and three sbd (single crossover) chromosomes were also tested and found not to carry recessive lethals. From In P^o cd^2/sbd In P^{sbd} ro, two ro, one sbd cd^2, two cd^2 ro, one sbd, and one + chromosome were tested and found not to carry recessive lethals. It follows that, if such crossover chromosomes were deficient for any genes, the deficiencies had no recessive lethal effects.

The second test was made by mating females heterozygous for two In P allelomorphs to males carrying recessive mutant genes in regions where the suspected deficiencies might be supposed to occur. The following mutant genes (with the loci given) were tested: sbd (58.2), ap (58.5), ss (58.5), bx (58.7), bx-b (59.5), sh-wing (60±), sr (62.0), gl (63.1), k (64±), e^s (70.7), ro (91.1). The females used in the tests all carried one In P^F chromosome; the other chromosome was In P, In P^{En}, In P^M, In P^o, In P^{sbd}, or In P^W, each of these 6 kinds of heterozygotes being tested against all 11 mutant genes, with the production of over 100 wild type offspring in every test. This may be taken as proof that no one of the mutant loci concerned lies in the inversion of In P^F but outside it in any of the other 6 allelomorphs, or outside it in In P^F and in it in any of the other 6. It further follows that no two of the 6 allelomorphs differ from each other with respect to the position of any of these loci; since, if any two did so differ, at least one of them would differ from In P^F.

NO SURVIVING SINGLE CROSSOVERS WITHIN INVERTED SECTIONS FOUND IN TRIPLOIDS

The data indicate that when reverse conjugation occurs, so that crossing over is possible in females heterozygous for inversions, the single crossover chromosomes do not give viable zygotes. As pointed out above, this result is not unexpected, since such single crossovers do not have the normal complement of genes or normal fiber-attachments. It seemed possible that they might survive in triploid zygotes, where their effect would be relatively less in quantitative terms. Two experiments designed to test this possibility have given negative results, but they can not be supposed to exclude the possibility, since the numbers are rather small and since the second chromosome was not tested at all.

Triploid females of the constitution H/In E e/In E e, mated to e males, gave 25 H triploid females and 140 H intersexes, none of them ebony. H/In P^{sbd} sbd ro/In P^{sbd} sbd ro triploids mated to sbd ro males gave 82 H triploid females, none of them sbd, and 2 of them ro, and 449 H intersexes, of which 3 were ro and none were sbd. In both cases the data suggest that the two like chromosomes conjugated and passed to opposite poles more often than on a chance distribution, so that more than two-thirds of the diploid eggs carried an H chromosome. This is especially clear in the first experiment, where there were 140 H intersexes to 18 e intersexes, and 34 e to 9 H males—2 to 1 being the expected ratio in each case with random conjugation and segregation.[1] This relation needs more detailed study, as it may throw light on the mechanism of conjugation and reduction; for the present purpose it need only be noted that it decreases the significance of the data, in as much as it is probable that H and In chromosomes conjugated relatively infrequently, thus decreasing the number of crossovers to be expected within the inverted sections.

GEOGRAPHICAL DISTRIBUTION OF CROSSOVER REDUCERS

The data on the chromosomes of known geographical origin are summarized in earlier sections of this paper. These data show that no reducers in chromosome I can be referred to stocks of known origin, though 12 strains tested (from Europe, the United States and the West Indies) gave the standard crossover values.

For the left limb of chromosome II, none of the 15 wild stocks tested for the purpose gave reducers; but $C_{II\ L\ Cy}$ is known to have come from Ann Arbor, Michigan, and $C_{II\ L\ N}$ from Liverpool, Nova Scotia.

Normal right limbs of chromosome II were found in 17 localities, $C_{II\ R\ Cy}$ at Ann Arbor, Michigan, and $C_{II\ R\ N}$ and allelomorphs at Liverpool, Nova Scotia; New Orleans, Louisiana; Kushla, Alabama; and Cienfuegos, Cuba. The data suggest that $C_{II\ R\ N}$ may in fact be commoner in the region from Louisiana to Cuba than elsewhere; but much more information will be necessary to establish such a conclusion, which is not in agreement with the results for any other type of crossover reducer. Even in this case, the occurrence in Nova Scotia is not favorable to an assumption of a southern distribution.

$C_{III\ L's}$ were found at Bloomington, Indiana; Georgetown, Texas; Olympia, Washington; Amity, Oregon. Normal left limbs of chromosome III were recovered from all 34 localities for which data are available. Since the four $C_{III\ L's}$ concerned have not been tested for allelomorphism, they are of little value in considerations concerning geographical distribution.

The results for the right limb of chromosome III (36 tested localities) are more extensive. In E is recorded only from Prague, Czechoslovakia; but it also occurred in stocks collected either near New York City or near Woods Hole, Massachusetts. In Mo was found at Bryn Mawr, Pennsylvania; Columbia, Missouri; New Orleans, Louisiana. In P was met with most often, the localities being Woodbury, Connecticut; Bloomington, Indiana; Olympia, Washington; Georgetown, Texas; Cienfuegos, Cuba; Ensenada, Porto Rico. There is no indication here that a given type of reducer has a special geographical range.

[1] In the sbd experiment the numbers were 449 H to 57 sbd among the intersexes and 96 sbs to 57 h among the males. The sbd character is evidently relatively more inviable in intersexes than in males, and it is difficult to judge as to the deviation from random segregation.

The data as a whole strongly suggest that the region where a stock is collected does not influence the likelihood of its containing a crossover reducer—either the general likelihood or that for any given reducer. If this conclusion be adopted, a corollary is that the same reducer must be supposed to have arisen independently in several regions. It is, in fact, difficult to see how this view can be avoided even if one does not accept the first-stated conclusion It is scarcely possible that the nine independently discovered In P allelomorphs (6 from the wild stocks enumerated above and 3 in mutant strains of untraceable geographical origin[1]) all trace to a single primary occurrence of the inversion concerned. If inversions arise as frequently as is suggested by these considerations, one may expect that such an event will occur in the laboratory, in flies in which the details may be studied genetically. In this direction lies one of the principal hopes of determining the mechanism whereby inversions arise.

IS THERE A CORRELATION IN OCCURRENCE OF C'S IN DIFFERENT REGIONS?

Of the 30 wild stocks tested for crossover reducers in chromosome III (table 1), 9 gave $C_{III's}$; 8 of these 9 were tested for chromosome II, and $C_{II\ R's}$ were found in two of them. Of the 21 stocks that gave no $C_{III's}$, 7 were tested for II and one of them gave a $C_{II\ R}$. There is here no indication that C's in the two chromosomes are correlated in their occurrence in wild stocks.

There were only two $C_{III\ L's}$ found in the stocks of table 1; both of these were in stocks that also carried $C_{III\ R's}$. Of the three $C_{III\ L's}$ found in other experiments, two were also associated with $C_{III\ R's}$. No $C_{II\ L's}$ appeared in the tested wild stocks; but the two that have been found in other experiments were both associated with $C_{II\ R's}$. Thus, taking both chromosomes together, 6 of the 7 known $C_{L's}$ were associated with $C_{R's}$, and $C_{R's}$ are found in not more than one-fifth to one-third of the stocks tested.

One may conclude that there is here a real correlation. The simplest hypothesis is that inversions usually arise through some kind of entanglement of the opposite limbs of a single chromosome, resulting in inversions in each of these limbs. It is difficult to picture such a process in detail, and it can only be taken as a possible suggestion. It is in agreement with the fact that no clear case of inversion has been reported in the X-chromosome, which has only one limb. Perhaps study of species with different chromosome groups may throw some light on the problem.

SUMMARY

1. Sixteen new crossover reducers are described, with their interrelations to each other and to the previously known types.

2. The fourteen $C_{III\ R's}$ discussed fall into three groups: the original "ebony" ($C_{III\ E}$) and one new allelomorph; $C_{III\ Mo}$, a type not before described, three occurrences of which are recorded; the "Payne" type, of which nine examples are described.

[1] Two other In P allelomorphs are not here described and are not included in these totals. One of these was received from Dr. R. L. King, the other was found in hairy stock. Both are of unknown geographical origin, and either may have an origin common with In P^{o}, In P^{sbd}, or In P^{M}.

3. The $C_{III\ E}$ type represents inversion of a section that extends from a point between stripe and ebony to the right end of the chromosome. The $C_{III\ Mo}$ type is apparently due to an inversion of similar but not identical length to that of $C_{III\ E}$. The $C_{III\ P}$ type represents inversion of a section between 9 and 26 units long, that includes cardinal but not stubble or rough.

4. The five known $C_{III\ L's}$ have not been analyzed, owing to failure to get mutant genes with them. Their occurrence shows a high correlation with that of $C_{III\ R\ P}$ allelomorphs.

5. Older data concerning $C_{II\ L\ N}$ and $C_{II\ R\ N}$ are summarized. Three new allelomorphs of $C_{II\ R\ N}$ are described. These are not proved to be inversions, though that is the most probable view for $C_{II\ R\ N}$.

6. A new allelomorph of $C_{II\ L\ Cy}$ is described. It is not identical with $C_{II\ L\ Cy}$, since $C_{II\ L\ Cy}/C_{II\ L\ Cy}$ gives much more crossing over than does $C_{II\ L\ Cy}/C_{II\ L\ T}$. These are inversions, including dumpy, but not Star or black.

Mutant Genes Referred To

	Symbol	chromosome	locus
aristapedia	ap	III	58.5
bithorax	bx	III	58.7
bithorax-b	bx-b	III	59.5
black	b	II	48.5
cardinal, cardinal-2	cd, cd^2	III	75.7
claret	ca	III	100.7
crossveinless	cv	I	13.7
curled	cu	III	50.0
Curly	Cy	II	?
curved	c	II	75.5
cut	ct	I	20.0
Delta	Δ	III	66.2
Dichæte	D	III	40.4
dumpy	dp	II	13.0
ebony, ebony-12	e, e^{12}	III	70.7
echinus	ec	I	5.5
forked	f	I	56.5
garnet	g	I	44.4
glass	gl	III	63.1
Hairless	H	III	69.5
hairy	h	III	26.5
kidney	k	III	64±
Lobe	L	II	72.0
Minute-g	Mg	III	101.2
orange, same as cardinal-2			
peach	p^p	III	48.0
plexus	px	II	100.5
purple	pr	II	54.5
rough	ro	III	91.1
roughoid	ru	III	0.0
scarlet	st	III	44.0
scute	sc	I	0.0
sepia	se	III	26.0
short-wing	..	III	60±
sooty	e^s	III	70.7
speck	sp	II	107.0
spineless	ss	III	58.5
Star	S	II	0.0
stripe	sr	III	62.0
Stubble, stubbloid	Sb, sbd	III	58.2
thread	th	III	42.2
vermilion	v	I	33.0
vestigial	vg	II	67.0

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II

TRANSLOCATIONS BETWEEN THE SECOND AND THIRD CHROMOSOMES OF DROSOPHILA AND THEIR BEARING ON ŒNOTHERA PROBLEMS

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With one plate and four diagrams

CONTENTS

II

TRANSLOCATIONS BETWEEN THE SECOND AND THIRD CHROMOSOMES OF DROSOPHILA AND THEIR BEARING ON ŒNOTHERA PROBLEMS

INTRODUCTION

This paper gives an account of genetic and cytological studies on four translocations involving the second and the third chromosomes of *Drosophila melanogaster*. Three of these translocations (here designated A, C and B) represent a type, not before described in *Drosophila*, that may be called reciprocal translocation. In each case the second and third chromosomes have exchanged parts, by a process recalling crossing over. The fourth translocation here described (E) represents another unusual type, in which a fragment of one chromosome (II) has become attached to another (III), but not to its end. The only previously known case of this sort is Bridges' (1923) incompletely described "Pale" translocation in *Drosophila*.

ORIGIN

Translocations A, C and B arose in X-ray experiments reported by Dobzhansky (1929 *a*). As already described, males heterozygous for Bristle (Bl, chromosome II) and Dichaete (D, chromosome III) were treated with Muller's (1928) "t-4" dose of X-rays, and were mated to untreated females that were yellow, with attached X-chromosomes, and eyeless^2 (chromosome IV). The resulting Bl D sons were mated to eyeless^2 females. Of 144 such matings, 32 were sterile; 112 showed independent segregation for sex, Bl, D and ey^2; 5 gave no recombinations for D and ey^2; 4 gave no recombinations for Bl and D. The five in which D and ey^2 gave no recombinations have been reported on already (Dobzhansky, 1929*a*, 1929*b*). From each of the four cultures showing complete association of Bl and D, Bl D males crossed to wild-type females gave again only Bl D and wild-type. Table 1 shows the results of such matings in this and following generations. These four strains were continued, and were arbitrarily designated A, B, C and D. Strain D was very infertile, and died out before it was analysed.[1] Strains A, B and C gave results to be described in detail in this paper.

Translocation E was found in another X-ray experiment (Sturtevant), but under circumstances that make it probable that it was present in the stock before the X-ray treatment was applied.

Males of the constitution Sb/D were obtained from a small mass culture (3D females and 4 Sb males), and were subjected to X-rays, as adults, in two lots on separate days. They were then mated to ru h st p ss e^s females, and the

[1] Flies heterozygous for translocation D had misshapen wings, short legs and abnormal venation, and were frequently wholly sterile (especially the females). They also often died soon after emergence as adults. No modifications in external characters have been detected in flies heterozygous for translocations A, B, C and E.

Sb daughters were back-crossed to ru h st p ss e^s males. Translocation E was detected in this generation, as a marked reduction in ru h st crossing over. The first series of treated males gave rise to no translocations (11 Sb daughters of two treated males tested); but many of the treated males were sterile, and the two fertile ones gave several aberrant offspring, including some flies that were judged to be haplo-IV. In this series, therefore, the X-rays may be supposed to have been effective. The second treatment, according to the setting of the machine and the time of exposure, should have been slightly more severe than the first, but it induced no sterility and no aberrant types were noted in the offspring of the treated males. Dr. M. Demerec treated some specimens of *Drosophila virilis* at the same time, and these also appeared to have been affected very little if at all. It seems probable therefore that there was something wrong with the X-ray machine and that the treatment was really very light. Two treated males of this series gave normal daughters (one and eight, respectively), one male gave two daughters carrying the translocation, and one mating of two treated males to several ru h st p ss e^s females gave one normal daughter and one carrying translocation. The three females here listed as carrying translocation were found to have very similar dominant reducers of crossing over in the left limb of III, but the descendants of two of them were discarded before it was found that in the third line (coming from one of the two sisters) this reduction was due to a translocation. It was therefore not possible to make a test of the identity of the three crossover reducers; there can, however, be little doubt that they were the same and that the translocation was already present in one of the males of the mating that gave rise to the treated specimens.

TABLE 1—*Progeny of wild type* ♀ × *Bl D (carrying translocation)* ♂

Translocation	Wild type	Bl	D	Bl D	Total
A.....	361	..	..	361	722
B.....	424	..	..	390	814
C.....	474	..	..	430	904
D.....	194	..	..	103	297

CROSSING OVER; LOCI OF THE TRANSLOCATIONS

Females were made up heterozygous for translocations A, B, C and E, respectively, and for a series of second chromosome genes (tables 2, 4, 6, 8) and, in other experiments, for a series of third chromosome genes (tables 3, 5, 7, 9). These females, mated to multiple recessive males, gave the data shown in the tables just cited. The crossover values are summarized in tables 24 and 25. The values in the cases of A and C are somewhat lower than the standard values for the intervals concerned; B gives an obvious reduction in crossing over in the left limb of chromosome II (al—dp, dp—b), while E gives a similar reduction in this region and also in the left limb of III (ru—h, h—st).

These data also show that, in the A and C experiments, Bl (chromosome II) acts as though it lay between st and p (chromosome III), indicating that the spindle-fiber regions of the two chromosomes are closely linked in the females. (The locus of the spindle-fiber attachment is known to lie in chromosome III

TABLE 2—*Translocation A*

$$\frac{\text{1 2 3 4 Bl (tr) 6 7}}{\text{al dp b pr 5 c px sp}} \quad \frac{\text{D tr}}{} \quad \text{♀} \times \text{al dp b pr c px sp} \ \text{♂}$$

Offspring (D disregarded)			
Non-crossovers		**Double crossovers**	
0	Bl	158	1, 5	al Bl c px sp	1
	al dp b pr c px sp	68		dp b pr	2
	Total	226	1, 6	al Bl px sp	4
Single crossovers				dp b pr c	2
1	al Bl	9	1, 7	al Bl sp	2
	dp b pr c px sp	9	2, 4	b pr Bl	1
2	al dp Bl	25	2, 5	al dp Bl c px sp	7
	b pr c px sp	41		b pr	15
3	al dp b Bl	5	2, 6	al dp Bl px sp	14
	pr c px sp	5		b pr c	14
5	Bl c px sp	37	2, 7	al dp Bl sp	2
	al dp b pr	23		b pr c px	1
6	Bl px sp	37	3, 6	pr c	1
	al dp b pr c	21	5, 6	Bl c	1
7	Bl sp	12	5, 7	Bl c px	2
	al dp b pr c px	5	6, 7	Bl px	1
	Total	229		Total	70
			Triple crossovers		
			1, 5, 6	dp b pr px sp	1
			2, 5, 6	b pr px sp	1
				Total	2
				Grand total	527

TABLE 3—*Translocation A*

$$\frac{\text{Bl tr}}{} \quad \frac{\text{1 2 D 3 4 tr 5 6 7}}{\text{ru h st p ss } e^s} \quad \text{♀} \times \text{ru h st p ss } e^s \ \text{♂}$$

Offspring			
Non-crossovers		**Double crossovers**	
0	D Bl	263	1, 2	h D Bl	3
	ru h st p ss e^s	307	1, 4	h st Bl	2
	Total	570		ru D p ss e^s	1
Single crossovers			1, 6	ru D Bl ss e^s	3
1	ru D Bl	92		h st p	3
	h st p ss e^s	112	1, 7	ru D Bl e^s	8
2	ru h D Bl	34		h st p ss	13
	st p ss e^s	40	2, 6	ru h D Bl ss e^s	1
3	ru h Bl	7		st p	2
	D st p ss e^s	9	2, 7	ru h D Bl e^s	2
4	ru h st Bl	7		st p ss	3
	D p ss e^s	11	4, 6	D p	1
5	D Bl p ss e^s	1		Total	42
6	D Bl ss e^s	17	**Triple crossovers**		
	ru h st p	23	1, 2, 6	ru st p	1
7	D Bl e^s	27	1, 3, 7	ru D st p ss	1
	ru h st p ss	45		Total	2
	Total	425	**Bl-tr crossovers**		
				Bl D	1
				Total	1
				Grand total	1040

TABLE 4—*Translocation B*

$$\frac{1\ 2\ (\text{tr})\ 4\ \text{Bl}\ 5\ 6\ 7}{\text{al dp b}\ 3\ \ \text{pr}\ \ \ \ \text{c px sp}} \quad \frac{\text{D tr}}{\ } \ \female \times \text{al dp b pr c px sp} \ \male$$

Offspring (D disregarded)			
Non-crossovers		**Double crossovers**	
0	Bl	277	1, 5	al Bl c px sp	3
	al dp b pr c px sp	147	1, 6	al Bl px sp	4
	Total	424		dp b pr c	1
Single crossovers		2, 5	al dp Bl c px sp	1
1	al Bl	7		b pr	4
	dp b pr c px sp	5	2, 6	al dp Bl px sp	4
2	al dp Bl	14		b pr c	5
	b pr c px sp	12	2, 7	al dp Bl sp	1
3	al dp b Bl	13	3, 5	pr	2
	pr c px sp	10	3, 6	al dp b Bl px sp	5
4	al dp b pr Bl	2	3, 7	pr c px	1
	c px sp	2	5, 6	Bl c	29
5	Bl c px sp	110		al dp b pr px sp	12
	al dp b pr	75	5, 7	Bl c px	12
6	Bl px sp	101		al dp b pr sp	4
	al dp b pr c	67	6, 7	Bl px	2
7	Bl sp	32		Total	90
	al dp b pr c px	12	**Triple crossovers**	
	Total	462	1, 5, 6	al Bl c	1
				Total	1
				Grand total	977

TABLE 5—*Translocation B*

$$\frac{\text{tr Bl}}{\ } \quad \frac{1\ 2\ \text{D}\ 3\ \ \ 4\ \ 5\ \ 6}{\text{ru h}\ \ \ \ \text{st (tr) p}\ \ \text{ss e}^s} \ \female \times \text{ru h st p ss e}^s \ \male$$

Offspring (Bl disregarded)			
Non-crossovers		2, 3	ru h D st p ss e^s	1
0	D	254	2, 4	ru h D p ss e^s	7
	ru h st p ss e^s	201		st	6
	Total	455	2, 5	ru h D ss e^s	14
Single crossovers			st p	14
1	ru D.	105	2, 6	ru h D e^s	10
	h st p ss e^s	87		st p ss	11
2	ru h D	43	3, 4	D st	4
	st p ss e^s	58	3, 5	D st p	2
3	ru h	6	3, 6	D st p ss	3
	D st p ss e^s	8		ru h e^s	2
4	ru h st	26	4, 5	D p	8
	D p ss e^s	22		ru h st ss e^s	7
5	ru h st p	31	4, 6	D p ss	5
	D ss e^s	49		ru h st e^s	7
6	ru h st p ss	31		Total	170
	D e^s	39	**Triple crossovers**	
	Total	505	1, 3, 5	ru D st p	1
Double crossovers		1, 4, 5	ru D p	3
1, 3	ru D st p ss e^s	2		h st ss e^s	2
	h	2	1, 4, 6	ru D p ss	3
1, 4	ru D p ss e^s	5	2, 4, 5	st ss e^s	1
	h st	8		Total	10
1, 5	ru D ss e^s	12		Grand total	1140
	h st p	7			
1, 6	ru D e^s	16			
	h st p ss	17			

TABLE 6—*Translocation C*

$$\frac{\text{1 2 3 4 Bl (tr) 6 7}}{\text{al dp b pr 5 c px sp}} \quad \frac{\text{D tr}}{} \quad \text{♀} \times \text{al dp b pr c px sp ♂}$$

Offspring (D disregarded)			
Non-crossovers		1, 7... al Bl sp	4
0.... Bl	227	2, 3.. b Bl	1
0.... al dp b pr c px sp	154	2, 3.. al dp pr c px sp	1
Total	381	2, 5.. al dp Bl c px sp	16
Single crossovers		2, 5.. b pr	14
1.... al Bl	29	2, 6.. al dp Bl px sp	18
1.... dp b pr c px sp	17	2, 6.. b pr c	20
2.... al dp Bl	79	2, 7.. al dp Bl sp	7
2.... b pr c px sp	95	2, 7.. b pr c px	4
3.... al dp b Bl	11	3, 5... pr	3
3.... pr c px sp	11	3, 6... pr c	2
4..... c px sp	1	3, 7... al dp b Bl sp	1
5.... Bl c px sp	59	5, 6.. al dp b pr px sp	1
5.... al dp b pr	65	5, 6.. Bl c	10
6.... Bl px sp	64	5, 7... Bl c px	2
6.... al dp b pr c	54	Total	130
7.... Bl sp	15	**Triple crossovers**	
7.... al dp b pr c px	10	2, 3, 5 b Bl c px sp	1
Total	510	2, 5, 6 al dp Bl c	3
Double crossovers		2, 5, 6 b pr px sp	5
1, 3... al pr c px sp	1	Total	9
1, 5.. al Bl c px sp	12	Grand total	1030
1, 5.. dp b pr	1		
1, 6.. al Bl px sp	6		
1, 6.. dp b pr c	6		

TABLE 7—*Translocation C*

$$\frac{\text{Bl tr}}{} \quad \frac{\text{1 2 D 3 4 tr 5 6 7}}{\text{ru h st p ss e}^s} \quad \text{♀} \times \text{ru h st p ss e}^s \text{ ♂}$$

Offspring			
Non-crossovers		1, 7.. ru D Bl e^s	10
0.... D Bl	322	1, 7.. h st p ss	16
0.... ru h st p ss e^s	302	2, 4... st Bl	1
Total	624	2, 6.. ru h D Bl ss e^s	1
Single crossovers		2, 6.. st p	7
1.... ru D Bl	92	2, 7.. ru h D Bl e^s	4
1.... h st p ss e^s	127	2, 7.. st p ss	10
2.... ru h D Bl	59	3, 6.. ru h Bl ss e^s	3
2.... st p ss e^s	63	3, 6.. D st p	1
3.... ru h Bl	5	3, 7... D st p ss	1
3.... D st p ss e^s	4	4, 6.. ru h st Bl ss e^s	1
4.... ru h st Bl	7	4, 6.. D p	1
4.... D p ss e^s	12	4, 7.. ru h st Bl e^s	2
5.... D Bl p ss e^s	3	4, 7.. D p ss	1
5.... ru h st	3	6, 7... D Bl ss	1
6.... D Bl ss e^s	32	Total	82
6.... ru h st p	23	**Triple crossovers**	
7.... D Bl e^s	37	1, 3, 7 ru D st p ss	1
7.... ru h st p ss	32	1, 4, 7 ru D p ss	1
Total	499	Total	2
Double crossovers		Grand total	1207
1, 4... h st Bl	2		
1, 6.. ru D Bl ss e^s	6		
1, 6.. h st p	14		

TABLE 8—*Translocation E*

$$\frac{1 \quad tr \quad 3 \quad 4}{al\ dp\ 2\ b \quad pr \quad c} \quad \frac{tr\ Sb}{} \ \text{♀} \times al\ dp\ b\ pr\ c\ \text{♂}$$

Offspring	
No crossing over between tr and Sb	Crossing over between tr and Sb
0.. Sb 566	0.. Wild type 164
0.. al dp b pr c 303	0.. al dp b pr c Sb 87
1.. al Sb 13	1.. al 2
1.. dp b pr c 8	1.. dp b pr c Sb 4
2.. al dp Sb 9	2.. al dp 5
2.. b pr c 9	2.. b pr c Sb 6
4.. c Sb 203	4.. c 47
4.. al dp b pr 133	4.. al dp b pr Sb 41
1, 4 al c Sb 4	1, 2 al b pr c Sb 2
1, 4 dp b pr 3	1, 4 al c 3
2, 4 al dp c Sb 5	1, 4 dp b pr Sb 5
2, 4 b pr 6	2, 4 al dp c 4
Total 1262	Total 370
	Grand total 1632

TABLE 9—*Translocation E*

$$\frac{tr}{} \quad \frac{1\ tr\ 2\ 3\ 4}{ru \quad h \quad st \quad p\ ss} \ \text{♀} \times ru\ h\ st\ p\ ss\ \text{♂}$$

Offspring	
Non-crossovers	
0.. Wild type 299	4.. ru h st p 66
0.. ru h st p ss 253	4.. ss 86
Total 552	Total 176
Single crossovers	Double crossovers
1.. ru 3	1, 4 h st p 1
1.. h st p ss 6	2, 4 st p 1
2.. ru h 1	3, 4 ru h st ss 2
3.. ru h st 9	3, 4 p 1
3.. p ss 5	Total 5
	Grand total 733

between the loci of st and p, close to p, and in the second chromosome at the locus of Bl.) In general, however, the occurrence of crossing over in both chromosomes renders this type of experiment unsatisfactory for determining loci of the translocations. A more easily analyzed experiment is one in which crossing over is prevented in one pair of chromosomes by the use of inverted sections. For example, translocation males are crossed to females carrying Cy $C_{II\ L}$ $C_{II\ R}$ (Curly wing, a dominant, and inversions in each end of chromosome II that suppress almost all crossing over) and a series of third-chromosome recessives. The F_1 females, translocation over Cy-multiple recessive,

are mated to multiple recessive males; the apparent locus of Cy in the series of third-chromosome genes shows the locus of the translocation in chromosome III (tables 11, 13, 15, 17).

Similar experiments were carried out using second chromosome multiple recessives with the combination Df $C_{III\ L}$ $C_{III\ R}$ (Deformed eye, a dominant, with crossover suppressors in each end of chromosome III). The results appear in tables 10, 12, 14 and 16 (table 16 is not of quite the same nature; see discussion below of the locus of E).

Crossover values shown in tables 10 to 17 will be discussed in a later section of this paper. Analysis of these tables shows the following loci are concerned:

Translocation	Chromosome II (apparent locus of Df)	Chromosome III (apparent locus of Cy)
A	Not separating from pr and Bl	Not separating from p
B	Between b and pr	Between st and p
C	Just to right of Bl	Between st and p
E	Not separating from b	Not separating from h

TABLE 10—*Translocation A*

$$\frac{1\ \ 2\ 3\ \ 4\ \text{Bl}\ \text{tr}\quad 7\ \ 8}{\text{al dp b pr}\quad 5\ \ 6\ \text{c px sp}} \quad \frac{\text{D}\quad \text{tr}}{C_{III\ L}\quad \text{Df}\quad C_{III\ R}} \quad \text{♀} \times \text{al dp b pr c px sp ♂}$$

Offspring			
Non-crossovers			
0	Bl D	268	
	al dp b pr c px sp Df	201	
	Total	469	
Single crossovers			
1	al Bl D	60	
	dp b pr c px sp Df	61	
2	al dp Bl D	160	
	b pr c px sp Df	245	
3	al dp b Bl D	18	
	pr c px sp Df	40	
6	al dp b pr Df	111	
	Bl D c px sp	156	
7	al dp b pr c Df	64	
	Bl D px sp	145	
8	al dp b pr c px Df	25	
	Bl D sp	63	
	Total	1148	
Double crossovers			
1, 2	dp Bl D	8	
1, 6	al Bl D c px sp	19	
	dp b pr Df	25	
1, 7	al Bl D px sp	17	
	dp b pr c Df	10	
1, 8	al Bl D sp	10	
	dp b pr c px Df	14	
2, 3	b Bl D	3	
2, 6	al dp Bl D c px sp	33	
	b pr Df	41	
2, 7	al dp Bl D px sp	40	
	b pr c Df	41	
2, 8	al dp Bl D sp	15	
	b pr c px Df	11	
3, 6	al dp b Bl D c px sp	1	
	pr Df	13	
3, 7	al dp b Bl D px sp	8	
	pr c Df	13	
3, 8	al dp b Bl D sp	1	
6, 7	Bl D c	27	
	al dp b pr px sp Df	16	
6, 8	Bl D c px	1	
	al dp b pr sp Df	11	
7, 8	Bl D px	1	
	Total	379	
Triple crossovers			
1, 2, 6	dp Bl D c px sp	3	
1, 2, 7	dp Bl D px sp	2	
1, 2, 8	dp Bl D sp	2	
1, 3, 7	dp b Bl D px sp	1	
1, 6, 7	al Bl D c	1	
	dp b pr px sp Df	1	
1, 6, 8	dp b pr sp Df	3	
2, 6, 7	al dp Bl D c	5	
	b pr px sp Df	12	
2, 6, 8	al dp Bl D c px	1	
	b pr sp Df	6	
2, 7, 8	b pr c sp Df	3	
	Total	40	
	Grand total	2036	

TABLE 11—*Translocation A*

Bl tr / $C_{II\,L}$ Cy $C_{II\,R}$ — 1 2 D 3 4 tr 5 6 7 / ru h st p ss e^s ♀ × ru h st p ss e^s ♂

Offspring			
Non-crossovers			
0	D Bl	276	
	ru h st p ss e^s Cy	238	
	Total	514	
Single crossovers			
1	ru D Bl	137	
	h st p ss e^s Cy	114	
2	ru h D Bl	58	
	st p ss e^s Cy	63	
3	ru h Bl	13	
	D st p ss e^s Cy	12	
4	ru h st Bl	10	
	D p ss e^s Cy	18	
6	D Bl ss e^s	39	
	ru h st p Cy	33	
7	D Bl e^s	42	
	ru h st p ss Cy	42	
	Total	581	
Double crossovers			
1, 2	h D Bl	4	
	ru st p ss e^s Cy	3	
1, 6	ru D Bl ss e^s	13	
	h st p Cy	18	
1, 7	ru D Bl e^s	29	
	h st p ss Cy	34	
2, 3	Bl	1	
2, 6	ru h D Bl ss e^s	9	
	st p Cy	14	
2, 7	ru h D Bl e^s	10	
	st p ss Cy	12	
3, 7	ru h Bl e^s	4	
	D st p ss Cy	2	
4, 6	ru h st Bl ss e^s	1	
	D p Cy	1	
4, 7	ru h st Bl e^s	1	
	Total	156	
Triple crossovers			
1, 4, 6	ru D p Cy	1	
1, 4, 7	ru D p ss Cy	1	
	Total	2	
	Grand total	1253	

TABLE 12—*Translocation B*

1 2 tr 5 Bl 6 7 8 / al dp b 3 4 pr c px sp — D tr / $C_{III\,L}$ Df $C_{III\,R}$ ♀ × al dp b pr c px sp ♂

Offspring			
Non-crossovers			
0	Bl D	236	
	al dp b pr c px sp Df	260	
	Total	496	
Single crossovers			
1	al Bl D	27	
	dp b pr c px sp Df	33	
2	al dp Bl D	28	
	b pr c px sp Df	30	
3	al dp b Bl D	22	
	pr c px sp Df	7	
4	al dp b Bl Df	20	
	D pr c px sp	25	
5	D c px sp	5	
	al dp b pr Bl Df	6	
6	Bl D c px sp	223	
	al dp b pr Df	180	
7	Bl D px sp	212	
	al dp b pr c Df	155	
8	Bl D sp	77	
	al dp b pr c px Df	30	
	Total	1080	
Double crossovers			
1, 6	al Bl D c px sp	11	
	dp b pr Df	10	
1, 7	al Bl D px sp	8	
	dp b pr c Df	10	
1, 8	al Bl D sp	7	
	dp b pr c px Df	2	
2, 4	D al dp pr c px sp	1	
	b Bl Df	2	
2, 5	b pr Bl Df	1	
2, 6	al dp Bl D c px sp	15	
	b pr Df	12	
2, 7	al dp Bl D px sp	1	
	b pr c Df	4	
2, 8	al dp Bl D sp	1	
3, 6	al dp b Bl D c px sp	5	
3, 7	pr c Df	3	
4, 6	al dp b Bl c px sp Df	15	
	pr D	3	
4, 7	al dp b Bl px sp Df	3	
	pr c D	4	
4, 8	al dp b Bl sp Df	1	
	pr c px D	1	
5, 6	al dp b pr Bl c px sp Df	1	
	D	1	
6, 7	Bl D c	52	
	al dp b pr px sp Df	22	
6, 8	Bl D c px	22	
	al dp b pr sp Df	16	
7, 8	Bl D px	10	
	al dp b pr c sp Df	4	
	Total	248	
Triple crossovers			
2, 6, 7	al dp Bl D c	1	
	b pr px sp Df	4	
2, 6, 8	b pr sp Df	1	
2, 7, 8	al dp Bl D px	1	
	b pr c sp Df	1	
3, 5, 7	pr Bl px sp Df	1	
3, 6, 7	pr px sp Df	1	
3, 7, 8	pr c sp Df	1	
	Total	11	
	Grand total	1835	

TABLE 13—*Translocation B*

$$\frac{\text{tr Bl}}{C_{II\,L}\ \text{Cy}\ C_{II\,R}}\ \frac{1\ 2\,D\,3\ \ 4\,tr\,5\ 6\ \ 7}{\text{ru h}\quad\ \text{st}\quad\ \text{p ss e}^s}\ \text{♀} \times \text{ru h st p ss e}^s\ \text{♂}$$

Offspring			
Non-crossovers			
0	D Bl	289	
	ru h st p ss e^s Cy	209	
	Total	498	
Single crossovers			
1	ru D Bl	112	
	h st p ss e^s Cy	114	
2	ru h D Bl	72	
	st p ss e^s Cy	66	
3	ru h Bl	18	
	D st p ss e^s Cy	20	
4	ru h st Bl	16	
	D p ss e^s Cy	30	
5	ru h st Cy	9	
	D Bl p ss e^s	7	
6	D Bl ss e^s	45	
	ru h st p Cy	57	
7	D Bl e^s	29	
	ru h st p ss Cy	44	
	Total	639	
Double crossovers			
1, 2	h D Bl	6	
	ru st p ss e^s	3	
1, 4	h st Bl	1	
	ru D p ss e^s Cy	4	
1, 5	ru h D Bl p ss e^s	2	
1, 6	ru D Bl ss e^s	17	
	h st p Cy	33	
1, 7	ru D e^s	22	
	h st p ss Cy	29	
2, 5	ru h D Bl p ss e^s	2	
2, 6	ru h D Bl ss e^s	9	
	st p Cy	17	
2, 7	ru h D Bl e^s	6	
	st p ss Cy	18	
3, 6	ru h Bl ss e^s	1	
	D st p Cy	1	
3, 7	ru h Bl e^s	1	
	D st p ss Cy	4	
4, 5	D Cy	2	
4, 6	D p Cy	2	
4, 7	D p ss Cy	3	
5, 7	D Bl p ss	1	
	ru h st e^s Cy	1	
6, 7	D Bl ss	2	
	ru h st p e^s Cy	2	
	Total	189	
Triple crossovers			
1, 3, 6	h ss e^s Bl	1	
2, 6, 7	ru h D Bl ss	1	
	Total	2	
	Grand total		1328

TABLE 14—*Translocation C*

$$\frac{1\ 2\ 3\ 4\ \text{Bl}\ \text{tr}\ 6\ 7\ 8}{\text{al dp b pr}\ \ 5\ \ \text{c px sp}} \quad \frac{\text{D}\quad\ \text{tr}}{\text{C}_{\text{III L}}\ \ \text{Df}\ \ \text{C}_{\text{III R}}} \ \female \times \text{al dp b pr c px sp} \ \male$$

Offspring		
Non-crossovers		
0	Bl D	210
	al dp b pr c px sp Df	167
	Total	377
Single crossovers		
1	al Bl D	57
	dp b pr c px sp Df	36
2	al dp Bl D	148
	b pr c px sp Df	159
3	al dp b Bl D	26
	pr c px sp Df	45
4	al dp b pr Bl D	1
	c px sp Df	2
5	Bl c px sp Df	2
6	Bl D c px sp	67
	al dp b pr Df	95
7	Bl D px sp	78
	al dp b pr c Df	73
8	Bl D sp	22
	al dp b pr c px Df	36
	Total	847
Double crossovers		
1, 2	Bl D dp	1
	al b pr c px sp Df	4
1, 6	Bl D al c px sp	6
	dp b pr Df	10
1, 7	Bl D al px sp	19
	dp b pr c Df	14
1, 8	Bl D al sp	9
	dp b pr c px Df	4
2, 3	Bl D b	5
	al dp pr c px sp Df	3
2, 5	al dp Bl c px sp Df	2
2, 6	al dp Bl D c px sp	24
	dp b pr Df	61
2, 7	al dp Bl D px sp	42
	b pr c Df	42
2, 8	al dp Bl D sp	18
	b pr c px Df	15
3, 6	al dp b Bl D c px sp	9
	pr Df	10
3, 7	al dp b Bl D px sp	19
	pr c Df	11
3, 8	al dp b Bl D sp	7
	pr c px Df	6
5, 6	Bl Df	3
6, 7	Bl D c	12
	al dp b pr px sp Df	13
6, 8	Bl D c px	7
	al dp b pr sp Df	7
7, 8	Bl D px	3
	al dp b pr c sp Df	3
	Total	389
Triple crossovers		
1, 2, 4	Bl D al b pr	1
1, 2, 7	al b pr c Df	1
1, 6, 8	dp b pr sp Df	6
2, 3, 6	b Bl D c px sp	2
	al dp pr Df	3
2, 3, 7	b Bl D px sp	6
	al dp pr c Df	9
2, 3, 8	Bl D b sp	1
2, 6, 7	b pr px sp Df	9
2, 6, 8	al dp Bl D c px	4
	b pr sp Df	4
2, 7, 8	b pr c sp Df	1
	Total	47
	Grand total	1660

TABLE 15—*Translocation C*

$$\frac{\text{Bl tr}}{C_{II\,L}\ \text{Cy}\quad C_{IIR}}\ \frac{1\ 2\ D\ 3\ 4\ tr\ 5\ 6\quad 7}{ru\quad h\quad\quad st\quad\quad p\quad ss\ e^s}\ \text{♀} \times ru\ h\ st\ p\ ss\ e^s\ \text{♂}$$

Offspring			
Non-crossovers			
0	D Bl	283	
	ru h st p ss e^s Cy	178	
	Total	461	
Single crossovers			
1	ru D Bl	134	
	h st p ss e^s Cy	99	
2	ru h D Bl	55	
	st p ss e^s Cy	54	
3	ru h Bl	12	
	D st p ss e^s Cy	17	
4	ru h st Bl	17	
	D p ss e^s Cy	13	
5	ru h st Cy	2	
	D Bl p ss e^s	5	
6	D Bl ss e^s	43	
	ru h st p Cy	44	
7	D Bl e^s	52	
	ru h st p ss Cy	45	
	Total	592	
Double crossovers			
1, 2	D Bl h	3	
	ru st p ss e^s Cy	2	
1, 4	h st Bl	2	
	ru D p ss e^s Cy	5	
1, 5	ru D Bl p ss e^s	3	
1, 6	ru D Bl ss e^s	18	
	h st p Cy	18	
1, 7	ru D Bl e^s	29	
	h st p ss Cy	23	
2, 6	ru h D Bl ss e^s	7	
	st p Cy	14	
2, 7	ru h D Bl e^s	8	
	st p ss Cy	12	
3, 7	ru h Bl e^s	1	
4, 6	ru h st Bl ss e^s	3	
	D p Cy	5	
4, 7	ru h st Bl e^s	1	
5, 7	ru h st e^s Cy	1	
6, 7	Bl D ss	1	
	Total	156	
Triple crossovers			
2, 3, 6	ru h D st p Cy	1	
	Total	1	
	Grand total	1210	

TABLE 16—*Translocation E*

$$\frac{1\quad tr\quad 3\quad 4}{al\ dp\ 2\quad b\quad\ pr\quad\ c}\ \frac{tr\quad\ Sb}{C_{III\,L}\ Df}\ \text{♀} \times al\ dp\ pr\ c\ \text{♂}$$

Offspring (Df disregarded)			
No crossing over between tr and Sb			
0	Sb	186	
	al dp b pr c	130	
1	al Sb	9	
	dp b pr c	10	
2	al dp Sb	7	
	b pr c	6	
4	al dp b pr	70	
	c Sb	79	
1, 2	al b pr c	1	
1, 4	al c Sb	8	
	dp b pr	4	
2, 4	al dp c Sb	1	
	Total	511	
Crossing over between tr and Sb			
0	Wild type	7	
	al dp b pr c Sb	10	
4	c	6	
	al dp b pr Sb	10	
2, 4	al dp c	1	
	Total	34	
	Grand total	545	

TABLE 17—*Translocation E*

$$\frac{\text{tr}}{\text{Cy}} \quad \frac{1\ \text{tr}\ 2\ \ 3\ 4}{\text{ru}\quad \text{h}\quad \text{st p ss}} \ \text{♀} \times \text{ru h st p ss} \ \text{♂}$$

Offspring			
Non-crossovers		Double crossovers	
0	Wild Type	418	1, 3 h st Cy	1
	ru h st p ss Cy	360	1, 4 ru ss	1
	Total	778		h st p Cy	3
Single crossovers			3, 4 ru h st ss Cy	2
1	ru	3		p	2
	h st p ss Cy	11	Total	9
2	ru h Cy	2	Grand total	1071
3	ru h st Cy	9		
	p ss	12		
4	ru h st p Cy	116		
	ss	131		
	Total	284		

In the case of E, the $C_{III\ R}$ was not present in the experiment with second chromosome recessives, so the locus in II is not evident from table 16. Tables 8 and 16 show no crossing over between b and pr in the presence of E, and other data show complete linkage of b and h (chromosome III). In another experiment, from translocation over b pr, a single translocation pr fly was obtained and a stock established from it, showing that the locus is to the left of pr.

MATINGS OF TRANSLOCATION × TRANSLOCATION—NON-DISJUNCTION OF TRANSLOCATED SECTIONS

The clearest genetic evidence as to the nature of the translocations has come from matings in which both parents were heterozygous for the same translocation and were also heterozygous for a series of loci in chromosomes II and III. These matings have shown that the complete linkage between the two chromosomes, observed in matings of translocation to wild type, is due, not to the absence of gametes resulting from recombination, but to the fact that such gametes form zygotes that are inviable because they do not have a normal complement of genes.

In the cases of translocations A and C, females of the constitution al dp Bl c px sp D translocation over al dp b pr c px sp were mated to males that were Bl ru h D ss e^s translocation over ru h st p ss e^s. If such flies produced only the two types of gametes that are viable in matings to wild type, the result should be 1 Bl D homozygote (dies, D being lethal): 2 Bl D heterozygotes: 1 wild type—plus a few Bl and D flies due to occasional crossing over between these loci and the translocation in the mother. These classes were in fact produced in about the expected proportions (table 18), but two other classes were also present—al dp Bl D ss e^s and Bl c px sp ru h D. The first class received both left limbs of chromosome II (designated "II L") from the

mother, and both right limbs of III (III R) from the father; the second received both II R's from the mother and both III L's from the father. As shown in an earlier section, the loci of the translocations in these two cases are close to Bl and to p, respectively; these loci are also known to lie close to the spindle-fibers, *i.e.*, to the middles of the two chromosomes.

TABLE 18—*Non-disjunction of sections of the second and the third chromosome*

$$\frac{\text{al dp Bl D}}{\text{al dp b pr c px sp}} \quad \frac{\text{c px sp}}{} \quad ♀ \times \quad \frac{\text{Bl D h ru}}{} \quad \frac{e^s \text{ ss}}{\text{ru h st p ss } e^s} \; ♂$$

	Bl D	Wild type	Bl D al dp ss e^s	Bl D ru h c px sp	Bl	D	Total
Translocation A.....	398	169	17	21	10	4	619
Translocation C.....	169	89	7	5	9	10	289

$$\frac{\text{Bl px sp}}{\text{al dp b pr c px sp}} \quad \frac{\text{D al dp}}{} \quad ♀ \times \quad \frac{e^s \text{ ss Bl}}{} \quad \frac{\text{ru h D}}{\text{ru h st p ss } e^s} \; ♂$$

	Bl D	Wild type	Bl D al dp ss e^s	Bl	D	Total
Translocation B.....	243	100	39	15	15	466

It follows from the non-disjunction results just stated, that the left limb of II is capable of passing, at segregation, to a different cell from the right limb of II—and likewise for III. One may conclude, then, that the loci of the translocations represent points at which the two chromosomes are broken in

TABLE 19—*Mating together individuals heterozygous for E translocation*

$$\frac{\text{Cy}}{} \quad \frac{|}{\text{D}} \quad ♀ \times \quad \frac{}{} \quad \frac{|}{\text{Sb}} \; ♂$$

Cy D Sb	Cy D	Cy Sb	D	Sb	Total
104	92	87	93	90	466

two. But in order to account for the linkage observed (in translocation × wild type) between II and III, it is necessary to suppose in addition that there has been fusion of at least one of the fragments of II to one of those to III. Finally, the cytological results (see below) show no increase in chromosome number, so that *both* fragments of II must be supposed to be joined of corresponding fragments of III.

The non-disjunction data fit the view that translocations A and C are due to an interchange of parts, such that II L and III L are attached and II R and III R are likewise attached—in each case the attachments occurring at the ends normally attached to other limbs, *i. e.*, at the breaking points.

Gametes 1 and 2 of Diagram 1 represent the two products of one reduction division and may be assumed to be equally frequent; likewise 3 and 4, 5 and 6. Table 20 shows that the frequencies of these types of maturation may be deduced from the wild type and the two non-disjunctional classes, respectively, in table 18. The wild type class is certainly relatively more viable than the two multiple-mutant classes concerned; nevertheless there can be no doubt, from the very great difference in frequency observed, that segregation of the 1, 2 type is far more frequent than the other two, *i. e.*, that opposite members of the cross-shaped configuration at the top of Diagram 1 usually pass to the same pole at maturation. Viability complications make the calculation of the

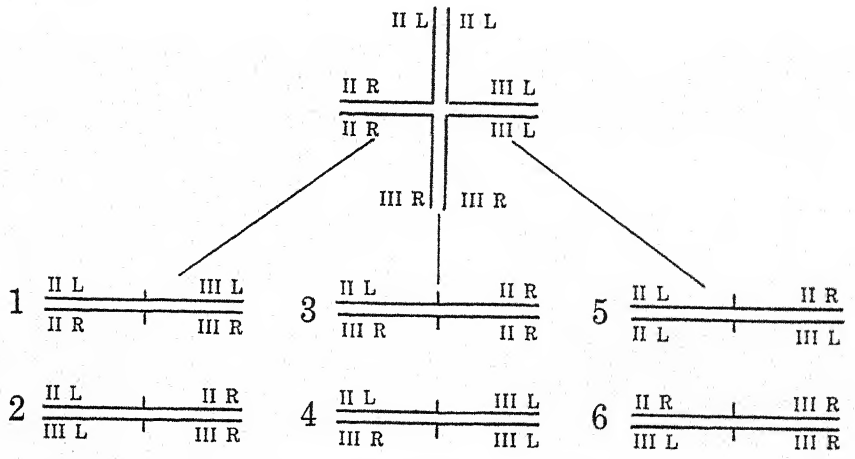


DIAGRAM 1—The six kinds of gametes produced by translocations A and C. II L and II R, the left and the right limbs of the second chromosome respectively. III L and III R, the left and the right limbs of the third chromosome respectively.

exact proportions of somewhat doubtful significance: apparently, however, the 1, 2, type occurs in about 60 per cent of the gametes.

Diagram 1 shows the chromosome complex of translocations A and C (as will be shown below, cytological observations bear out this figure) and the 6 types of gametes produced. Table 20 shows the result of mating together two such individuals. Class 1, homozygous for the translocation, is known from other experiments (see below) not to be viable. Classes 2 and 7 include individuals like the parents (the Bl D of table 18). Class 8 includes individuals with no abnormal chromosomes (the wild type of table 18). Class 3 has only one III L and three III R's; class 4 has only one II R and three III L's. They may be assumed to die, and similar discrepancies occur in all the other classes (except number 1) labeled "dies" in the table. Classes 16 and 21

receive both III L's from one parent and both II R's from the other parent (Bl c px sp ru h D and a like number of Bl D of table 18). Classes 30 and 35 receive both II L's from one parent and both III R's from the other (al dp Bl D ss e^s and a like number of Bl D in table 18).

The matings of translocation B × B differed from those of A and C in that the mothers were not homozygous for curved: ♀ al dp Bl px sp D translocation over al dp b pr c px sp × ♂ Bl ru h D ss e^s translocation over ru h st p ss e^s. Again there were produced Bl D and wild type, the former rather more than twice as numerous as the latter, and a few Bl and D due to crossing over. But there was only one class showing recessive genes, namely al dp Bl D ss e^s (table 18). This class shows that II L and II R, III L and III R are again capable of segregating separately, as in A and C. The data on the loci of the translocation given above show that the breaking points are both somewhat to the left of those in A and C—about 2 units to the right of b in II and rather less than 2 units to the left of p in III. The difference in the case of III is probably less significant than that in II, as

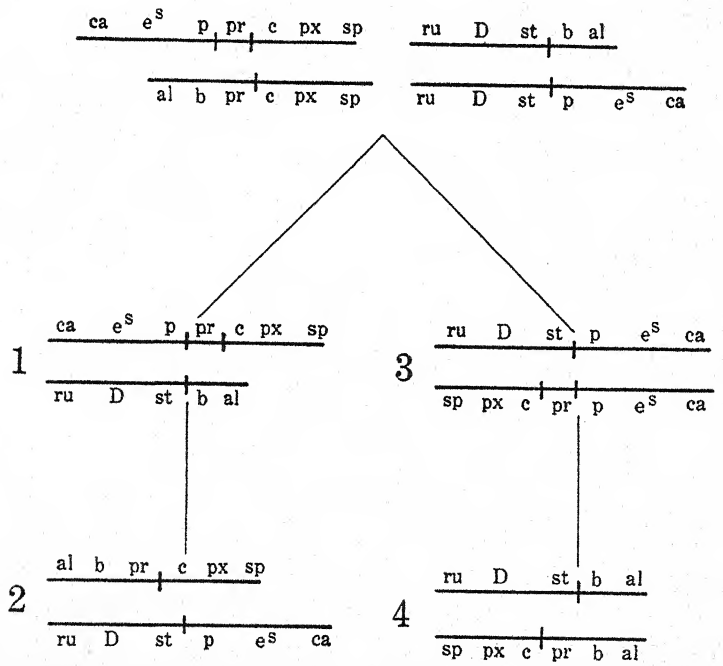


DIAGRAM 2—The four kinds of gametes produced by translocation B.

shown by the further analysis. Here again cytological study (see below) has shown no increase in number of chromosomes, so that both fragments of II must be supposed to have fused with corresponding fragments of III. Why, then, the different genetical results from those observed with A and C? The

exceptional class observed is non-disjunctional for II L and III R; the fragment represented by II L is shorter here than in the case of translocations A and C, while III R is attached to a longer portion (II R) than in the case of translocations A and C. Diagram 2 and table 21 show the analysis that fits the observed data. II L is attached to III L, II R to III R; but II R includes the middle of the chromosome and always passes to the opposite pole (at reduction) from the normal (II L II R) chromosome. There result four types of gametes, instead of the six that were found in the A and C cases.

The mating of translocation E × E was made as follows: Cy D over translocation female × Sb over translocation male. There resulted five classes, in nearly equal numbers (table 19): Cy D Sb, Cy D, Cy Sb, D, Sb. Other experiments, not here recorded in detail because they suffer from viability complications and were done on a small scale, have involved matings

TABLE 20—*Results of inbreeding translocations A or C*

	1 II L, III L II R, III R	2 II L, II R III L, III R	3 II L, II R III R, II R	4 II L, III L III R, III L	5 II L, II R II L, III L	6 II R, III R III L, III R
1′ {II L, III L / II R, III R	1 Homozygous translocation (dies)	2 Heterotranslocation	3 dies	4 dies	5 dies	6 dies
2′ {II L, II R / III L, III R	7 Heterotranslocation	8 Wild type	9 dies	10 dies	11 dies	12 dies
3′ {II L, II R / III R, II R	13 dies	14 dies	15 dies	16 Non-disj. III L, II R	17 dies	18 dies
4′ {II L, III L / III R, III L	19 dies	20 dies	21 Non-disj. II R, III L	22 dies	23 dies	24 dies
5′ {II L, II R / II L, III L	25 dies	26 dies	27 dies	28 dies	29 dies	30 Non-disj. III R, II L
6′ {II R, III R / III L, III R	31 dies	32 dies	33 dies	34 dies	35 Non-disj. II L, III R	36 dies

of flies heterozygous for translocation E and homozygous for various recessives to other specimens heterozygous for E but not carrying these recessives. None of the third-chromosome recessives have ever appeared in F_1 from such matings; in chromosome II al, dp and d have appeared,[1] but pr, c, px and sp

[1] Females heterozygous for al dp have given a few "equational" exceptions—al and al dp, but never dp. This confirms the view that the translocated al-dp-d fragment is attached by the d end, at which the break occurred.

have never done so. That is, translocation E gives non-disjunction only for II L. The data in the preceding section indicated loci for E even further to the left of the spindle fibers than in the case of B, so that it is reasonable to suppose that the central regions of both II and III would show normal segregation and no non-disjunction. If this be so, II L, being the only portion that shows non-disjunction, must segregate separately from the middle of II and must be attached to III at h.

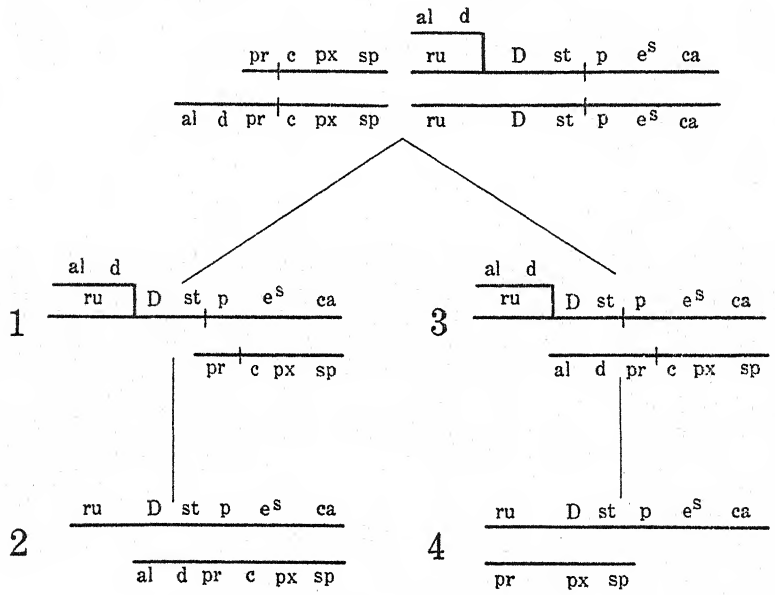


DIAGRAM 3—The four kinds of gametes produced by translocation E.

Diagram 3 and table 22 show that this interpretation fits the data of table 19. The substantial equality of the five classes produced shows that segregation of II and III must be practically independent, *i.e.*, the four types of gametes shown in Diagram 3 must be produced in nearly equal numbers.[1]

Diagram 4 summarizes the conclusions as to the constitutions of the four translocations.

[1] A curious corollary of this analysis may be noted here. The Cy Sb flies of table 19 received Cy from their mothers, Sb from their fathers. Yet, if such flies (males) are mated to wild-type flies, Cy and Sb will appear to be completely linked; since all the Cy not-Sb flies will have II L represented three times and all the Sb not-Cy will have it represented only once, such flies will die. The apparent result therefore is 100 per cent crossing over. Such results have in fact been obtained with translocation E.

TABLE 21—*Translocation B*

Bl px sp / al dp b pr D dp al / c px sp × e^s ss Bl ru h D / ru h st p ss e^s

	1 Bl px sp / D al dp	2 al dp b pr / c px sp Bl px sp	3 Bl px sp	4 al dp b pr / c px sp / al dp D
1′ e^s ss Bl / ru h D	1 dies	2 Bl D	3 dies	4 dies
2′ ru h st p ss e^s	5 Bl D	6 Wild type	7 dies	8 dies
3′ ru h st p ss e^s / e^s ss Bl	9 dies	10 dies	11 dies	12 al dp Bl D ss e^s
4′ D ru h	13 dies	14 dies	15 Bl D	16 dies

TABLE 22—*Translocation E*

Cy D × Sb

	1	2 D / Cy	3 Cy	4 D
1′	Homozygous translocation (dies)	Cy D	dies	dies
2′ Sb	Sb	Cy D Sb	dies	dies
3′	dies	dies	dies	D
4′ Sb	dies	dies	Cy Sb	dies

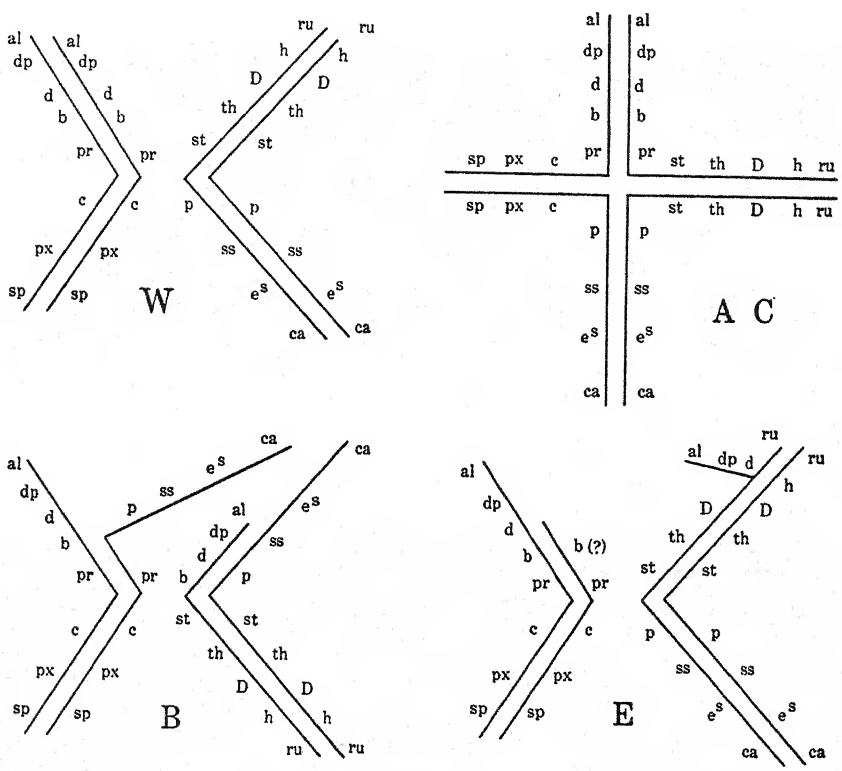


DIAGRAM 4—Schematic representation of the structure of the second and third chromosomes in wild type and in flies heterozygous for the different translocations. W, wild type; A, C, A and C translocations; B, B translocation; E, E translocation.

CYTOLOGICAL STUDY OF THE TRANSLOCATIONS

Cytological study of the four translocations has been made, using ovaries of heterozygous females. The best oögonial plates seen are reproduced in Plate 1, except those for translocation E, which are not figured.

Figures 1 to 7 (translocation A) and 8 to 14 (translocation C) agree in appearing at first glance to be like normal *melanogaster* female figures, with a pair of rods, a small spherical pair, and four V-shaped chromosomes. More careful examination shows that in not one of these figures are the four V-shaped chromosomes arranged in two pairs each with the two members parallel throughout their length—which is the most common arrangement in normal females. Figure 11 suggests such an arrangement; but the preparation itself does not look so at all, as the two shorter limbs near the center of the figure are in reality directed upward, nearly at a right angle to the rest of the plate. Figures 11 and 4 really represent the cross-shaped arrangement shown in Diagram 4; figures 2 and 8 also approximate it.

It is known (Dobzhansky, 1929*a*) that chromosome III is, cytologically, longer than II. The genetical data show that translocations A and C repre-

sent exchanging of halves of these chromosomes. The expectation then would be that the figures would show the two equal-armed chromosomes—a shorter one (normal II) and a longer one (normal III)—and two unequal-armed ones (II L III L and II R III R). These differences are not striking enough to be made out in detail, but unequal-armed chromosomes can be identified in some cases (*e.g.*, figures 1, 13, 14), and chromosomes unequal in length can also be seen (especially clear in figures 2, 3, 12).

Dr. C. W. Metz has undertaken a cytological study of the maturation divisions of translocations A and C. This study is not yet completed, but he informs us that preliminary results indicate that, in males heterozygous for the translocations, the four large autosomes occur in one tangled mass in late prophases of the first maturation division, rather than in two such aggregates (as is the case in normal males).

Figures 15 to 18 are from translocation B.

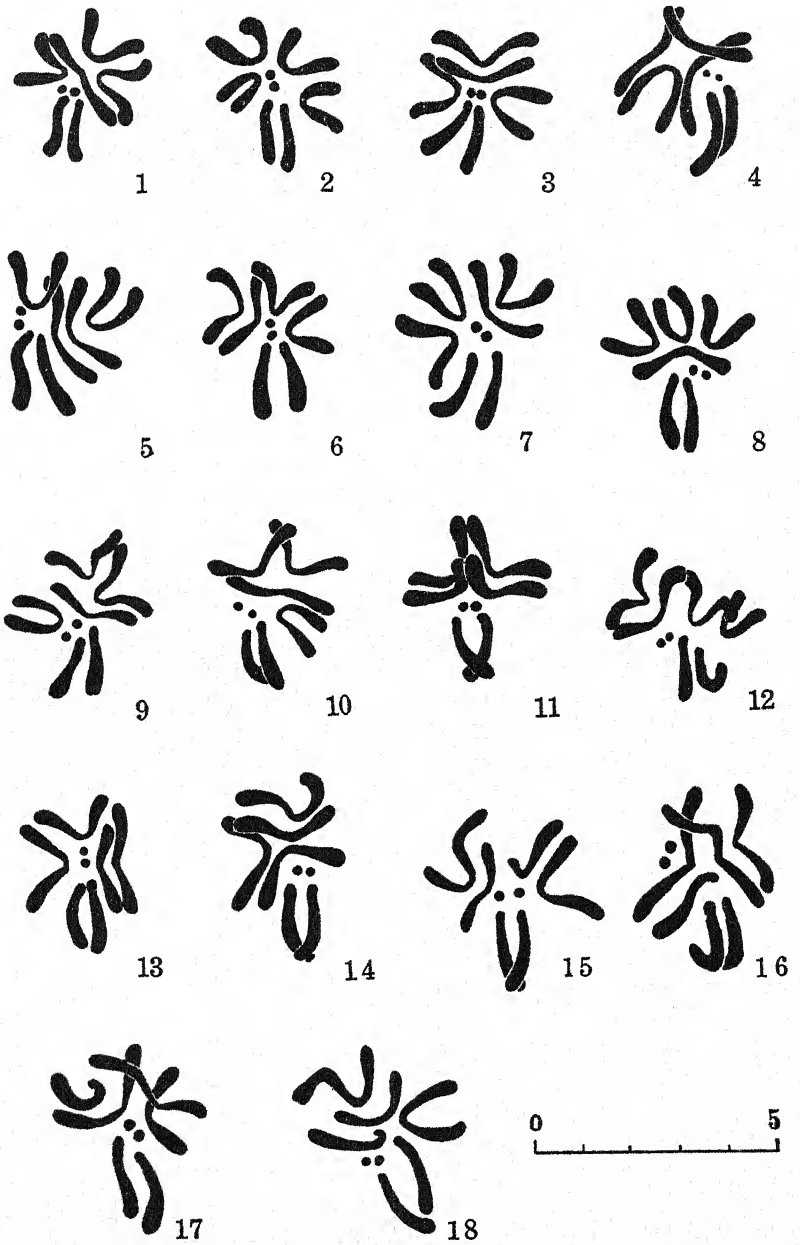
In each of them there is a long V-shaped chromosome (III), and in figures 15, 16 and 17 the mate of this is a J-shaped chromosome (present but not paired with III in figure 18). A normal II is also present, and has as its mate the longest chromosome in the figures. This long chromosome is always unequal-armed, with a conspicuous bend near the middle of the longer arm. These results are evidently in good agreement with the relations indicated in Diagram 4.

The cytological study of translocation E yielded an unexpected result; the chromosomes were not distinguishable from those of wild type. Two separate series of females, from different sources, gave the same result; errors in selecting specimens for study are thus rendered altogether improbable. The only conclusion to be drawn is that the section from al to d (Diagram 4) is too small to be observed under these conditions. It may be noted that the cytological results from translocation B show that the longer section from al to b, that is there attached to III L, constitutes only a small part of the mass of II L, *i.e.*, the short limb of the J-shaped chromosome of figures 15 to 18.

MORTALITY AMONG OFFSPRING OF TRANSLOCATIONS

When flies heterozygous for any of the four translocations are mated to wild type, only two types of offspring are produced—one class with normal chromosomes and another with both II and III abnormal as in the translocation parent. Yet the data from translocation × translocation show that from four to six kinds of gametes are produced by translocation flies. The recombination classes have abnormal complements of genes, and would be expected to die; in the cases of A, B, and C there is direct evidence, not only that they die, but that the death occurs for the most part before emergence of the larvæ from the eggs. Table 23 shows the results of egg-counts made from matings of wild-type female by translocation male.

In the cases of A and C, about 60 per cent of the eggs laid gave rise to adult offspring. As shown in Diagram 1, translocation A or C males give six types of sperm; of these only those labeled 1 and 2 in the diagram give viable offspring with wild-type females. As was pointed out in the discussion of tables 18 and 19, these two types of sperm are formed much more frequently than are numbers 3 to 6—a conclusion which is in agreement with the 60 per



The drawings represent chromosomes (oögonial plates) of the females carrying translocations in heterozygous condition. Fixation, strong Flemming's fluid: stain, iron hematoxylin. All drawings were done with the aid of a camera lucida, under Zeiss immers. 30, at the level of the work-table. The scale given in the plate represents 5μ.

Figures are placed so that the X-chromosomes occupy the lower part of the drawing. Figures 1 to 7 represent A translocation, figures 8 to 14 C translocation. Notice the disturbance of the somatic pairing of the V-shaped autosomes. Figures 15 to 18 represent B translocation. The J-shaped chromosome in these figures is the left limb of the third chromosome with a section of the second chromosome attached to it; the longest and unequal-armed chromosome is the deficient second chromosome with the right limb of the third chromosome attached to it.

cent survival shown in table 23. In the case of translocation B only four types of sperm are formed (Diagram 2); the analysis of table 21, compared

TABLE 23—*Mortality in the progeny of Wild type* ♀ × *Bl D (carrying translocations)* ♂

Translocation	Eggs laid	Larvæ	Pupæ	Imagines	Survived
					p. ct.
A	270	189	164	163	60.4
B	274	144	135	131	47.8
C	331	220	206	198	59.8

with the data of table 18, indicates that the four types are more nearly equal in number than are the six types from A and C (relation between wild type and al dp Bl D ss e^s classes of table 18, in connection with which there must be supposed to be a distinct viability difference in favor of the wild-type class). Table 23 shows 48 per cent survival in matings of wild-type × translocation B; 50 per cent would correspond to equal frequencies of the four types of sperm. It is probable, however, that incidental mortality not connected with the abnormal chromosome groups is present in any such experiment, so that it is likely that the true survival percentage for B is distinctly above 50 per cent, *i.e.*, that sperm of types 1 and 2 (Diagram 2) are more frequently formed than are those of types 3 and 4. This conclusion is also in better agreement with the data of table 18, where the entire difference in numbers of wild type as opposed to al dp Bl D ss e^s seems not likely to be due to differential viability.

It was assumed, in discussing the results of mating translocation × translocation, that homozygous translocation dies. This is an experimentally demonstrated fact: Cy over translocation males and females have been mated together with the production of nothing but Cy flies. This test has been carried out for all four translocations. The result need not have been expected, as homozygous translocations apparently should have a complete (double) set of genes, with no duplications or deficiencies. This lethal effect nevertheless appears to be usual for translocations (see Dobzhansky, 1929*b*). Several possible interpretations may be suggested, but the present cases do not throw any new light on the problem.

It has been shown that translocations A and C are very similar in behavior; there was some fear that they might actually have been confused in the records, so that the two tested strains were really the same. Accordingly an attempt was made to get flies heterozygous for both—translocation A over translocation C.

The attempt was fully successful, such flies being quite viable, and showing that the lethal effects of the two are due to different causes.

EFFECTS OF PREVENTING CROSSING OVER IN ONE CHROMOSOME ON CROSSING OVER IN THE OTHER CHROMOSOME

Tables 2 to 17 give a series of data on crossing over in chromosome II with and without crossover reducers in III, and on crossing over in III with and without reducers in II. These data are summarized in tables 24 and 25.

While no direct control data are available, inspection of the crossover values (with no reducers present) indicates that the translocations in general give less crossing over than the standard amount. It was suspected that this might be due to interference with normal synapsis, due to attraction of part of a

TABLE 24—*Crossing over in second chromosome (showing effects of preventing crossing over in third chromosome by* $C_{III\ L\ P}$ $C_{III\ R\ P}$)

Translocation A								
Interval	al-dp	dp-b	b-pr	pr-Bl	Bl-tr-c	c-px	px-sp	Total
With C_{III}	11.6	31.0	4.8	0.0	23.9	20.0	8.2	99.5
Without C_{III}	5.7	24.9	2.1	.2	17.1	18.4	4.7	73.1
Difference	+5.9	+6.1	+2.7	−.2	+6.8	+1.6	+3.5	+26.4

Translocation C								
Interval	al-dp	dp-b	b-pr	pr-Bl	Bl-tr tr-c	c-px	px-sp	Total
With C_{III}	10.1	34.0	9.8	0.2	0.4 21.2	21.4	9.2	106.3
Without C_{III}	7.4	25.6	3.1	.1	18.6	18.3	4.2	77.3
Difference	+2.7	+8.4	+6.7	+.1	+3.0	+3.1	+5.0	+29.0

Translocation B								
Interval	al-dp	dp-b	b-tr tr-pr	pr-Bl	Bl-c	c-px	px-sp	Total
With C_{III}	5.9	5.6	2.2 4.1	0.8	32.4	27.1	9.5	87.6
Without C_{III}	2.1	4.2	3.2	.4	25.9	23.6	6.6	66.0
Difference	+3.8	+1.4	+3.1	+0.4	+6.5	+3.5	+2.9	+21.6

Translocation E					
Interval	al-dp	dp-tr-b	b-pr	pr-c	Total
With C_{III}	5.9	2.9	0.0	32.8	41.6
Without C_{III}	2.7	2.8	.0	27.8	33.3
Difference	+3.2	+.1	.0	+5.0	+8.3

composite chromosome to II and of another part to III. The data of tables 24 and 25 were collected in an attempt to test this, by reducing the attraction to III (C_{III} experiment) and studying crossing over in II (table 24); and reducing the attraction to II (C_{II} experiment) and studying crossing over in III (table 25).[1]

[1] The $C_{II\ L}$, $C_{II\ R}$, and $C_{III\ R}$ are all known to be inverted sections; the $C_{III\ L}$ may be one.

The results were striking. In the case of A and C crossing over was brought up to normal (or approximately so) in each chromosome by cutting out the influence of the other chromosome, the "C" experiments giving about $\frac{4}{3}$ as much crossing over as their controls. In the cases of B and E, the C_{III}'s gave

TABLE 25—*Crossing over in third chromosome (showing effects of preventing crossing over in second chromosome by $C_{II\,LC_{II}}$ $C_{II\,RC_{II}}$)*

Translocation A

Interval	ru-h	h-D	D-st	st-tr tr-p	p-ss	ss-e^s	Total
With C_{II}	28.3	13.9	2.6	2.6	10.3	14.1	71.8
Without C_{II}	23.0	8.3	1.6	2.1 .1	4.9	9.5	49.5
Difference	+5.3	+5.6	+1.0	+0.4	+5.4	+4.6	+22.3

Translocation C

Interval	ru-h	h-D	D-st	st-tr	tr-p	p-ss	ss-e^s	Total
With C_{II}	27.8	12.9	2.6	3.8	0.9	12.6	14.3	74.9
Without C_{II}	22.3	12.0	1.2	2.3	0.5	7.5	9.6	55.4
Difference	+5.5	+.9	+1.4	+1.5	+.4	+5.1	+4.7	+19.5

Translocation B

Interval	ru-h	h-D	D-st	st-tr tr-p	p-ss	ss-e^s	Total
With C_{II}	25.9	15.1	3.5	4.4 1.8	14.2	12.3	77.2
Without C_{II}	23.7	14.5	2.7	10.0	13.2	12.6	76.7
Difference	+2.2	+.6	+.8	−3.8	+1.0	−.3	+.5

Translocation E

Interval	ru-h	h-tr-st	st-p	p-ss	Total
With C_{II}	1.4	0.3	2.3	21.4	25.4
Without C_{II}	1.8	0.2	2.4	23.8	28.2
Difference	+.4	−.1	+.1	+2.4	+2.8

a definite increase of crossing over in II, apparently bringing it up to normal in II R, and increasing it, but still leaving it distinctly below normal in II L; C_{II}'s were without effect on crossing over in III.

These results are intelligible on the basis of the supposition that led to the experiments, and are in good agreement with the findings as to somatic pairing of the chromosomes. The only case not entirely in accord is that one might

have supposed B would show low crossing over in III L when C_{II}'s were not used, since Diagram 4 and figures 15 to 18 suggest that some difficulties in synapsis might occur here.

BEARING OF RESULTS ON PROBLEMS CONCERNING SYNAPSIS AND REDUCTION

The study of translocations and other anomalies of chromosome makeup (*e.g.*, polyploidy, heteroploidy, inversion) is perhaps the most promising method of attack on the problems concerning the mechanism of synapsis, crossing over and reduction. The results of the present study that bear on these questions may be discussed under three headings: the cytological observations on somatic pairing, the effect of the translocations on crossing over and the frequency of occurrence of the different kinds of gametes produced.

The cytological observations agree with those of Painter and Muller (1929) and of Dobzhansky (1929*b*) in indicating that the somatic pairing characteristic of the Diptera is due to an attraction of like parts of chromosomes, rather than to properties of entire chromosomes. In the cases of translocations A and C this is especially striking, for of the four large V-shaped chromosomes, each has one limb like one of the others and the other limb like another one, yet in general size and shape the four are so nearly alike that it is, in most figures, not possible to identify them all. The somatic pairing is quite different from that of the superficially similar wild-type fly, and approximates more or less closely to the cross-shaped arrangement of Diagrams 1 and 4 (A,C), that is expected if like segments lie parallel to each other.

Females heterozygous for any one of the translocations gave somewhat reduced values for crossing over throughout both the second and the third chromosomes; with the single unexplained exception that translocation B apparently caused no reduction in the left limb of chromosome III.[1] These reductions are most simply explained as results of an interference with normal synapsis, due to the attraction of one chromosome to parts of two other chromosomes. Similar results were found by Dobzhansky (1929*a*), in a study of translocations of fragments of chromosome III to chromosome IV. In the present case this interpretation was tested, by interfering with conjugation of one possible type (through the introduction of inverted sections), and studying the crossing over resulting from the other possible type of conjugation. The result was definite; crossing over was increased in one chromosome by the presence of inverted sections in the other one. The one exceptional result was that inversions in II had no appreciable effect on crossing over in III in the case of translocation E. This exceptional result may be due to the fact that in E there is a piece of II attached to III subterminally, forming a Y-shaped chromosome which may react differently from the rod-shaped chromosomes present in every other case. In general, however, it is clear that interfering with conjugation of one part of a composite chromosome increases the crossing over between the rest of the composite and its unmodified mate.

The data from matings of translocation × translocation show that the possible kinds of gametes are formed with different frequencies. In the case

[1] In the case of translocation E the data for the two right limbs are not extensive, and it is quite possible that there is no real reduction—a result that is in no way inconsistent with the nature of this translocation.

of E, where a relatively small portion of II is attached to III, the remaining major portion of II always segregates from the normal II; III with attached portion of II always segregates from the normal III; and these two events are approximately independent; that is to say, the translocation does not affect the segregation of the greater portion of chromosomal material.

Translocation B represents exchange of the left half of III for a portion of the left limb of II that is rather larger than the portion concerned in E. The data show that the composite including III L and more than half of II always segregates from the normal II, and the other two chromosomes concerned (III R and smaller fragment of II, normal III) also always segregate. These two events are not independent, the two III R's usually passing to opposite poles.[1] Here the major portion of chromatin (more than half of II) segregates normally. The remaining two chromosomes pass to opposite poles, but are strongly influenced also by the behavior of the first pair, in such fashion that each member of the second pair usually passes to the opposite pole from that member of the first pair with which it has most in common. These results are probably to be referred back to what happens at synapsis.

Translocations A and C represent exchanges of half chromosomes between II and III. Each chromosome may be taken to be approximately equally like two of the others. The data show that it usually passes to the opposite pole from both of these; one pole has II L II R and III L III R; the other, II L III L and II R III R. In addition, two other types of segregation sometimes occur; II L II R and II L III L separating from II R III R and III L III R; II L II R and II R III R separating from II L III L and III L III R. These are far less frequent than the first type of segregation. The data suggest that the two are equally frequent, though the viability complications are so great that this latter conclusion must be taken as only an approximation. One of the two composite chromosomes must be supposed to have a spindle-fiber attachment-point that came originally from chromosome II, the other from III. It is therefore evident that these points are of no special importance in determining the orientation of the chromosomes on the reduction spindle, for if they were the two types of reduction here under discussion would not be approximately equal in frequency. It may be concluded that there is probably no specificity of the spindle-fibers, though their attachment-points are well known to be permanent in the same sense that genes have permanent positions in the chain of loci that makes up a genetic chromosome.

BEARING OF RESULTS ON ŒNOTHERA PROBLEMS

Belling (1927; Belling and Blakeslee, 1924, 1926) has developed an hypothesis, to account for certain aberrant trisomic types of Datura, that depends on the assumption of interchange of parts between non-homologous chromosomes, similar to that demonstrated in the present paper. This hypothesis is based largely on cytological study of the first maturation division and on the genetical data of Blakeslee that are still largely unpublished. This evidence indicates that like ends of chromosomes are attached to each other at the

[1] As shown by the greater frequency of wild type than of al dp Bl D ss e^8 in table 18. The expected viability differences here are very great, due chiefly to dp; another experiment, similar except that it included no second-chromosome recessives, gave 184 Bl D, 80 wild type, 23 Bl D ss e^8, 3 Bl, 2 D. The difference (80 to 23) here is certainly significant.

metaphase of the first maturation division, and that, following interchange of parts, the two ends of a chromosome may be like (and be attached to) ends of two other chromosomes that are not homologous to each other. Belling indicated the possible bearing of this view on the rings of chromosomes described by Cleland (1923, 1928) and others for *Œnothera* and other plants. Håkansson (1928), Darlington (1929) and Cleland and Blakeslee (1930) have elaborated this application in some detail.

The present results are lacking in one important respect—we do not know whether rings are formed at maturation or not. But the somatic pairing characteristic of the Diptera enables us to judge, from the oögonial configurations, that rings are probable in the cases of translocations A and C. The genetic data here are, however, of some importance in evaluating the hypothesis of chromosomal interchange as an interpretation of the peculiar behavior of *Œnothera*.

In translocations A and C, the two parental types of gametes are formed much oftener than are the other types. That is to say, if rings are formed, then adjacent members usually pass to opposite poles—as the cytological evidence shows in the case of *Œnothera*. Crossing over is less in flies heterozygous for translocations A and C than in normal flies; the evidence suggests that such is probably the case in *Œnothera*, since crossing over of the frequencies described by Shull (1923) can scarcely be supposed to occur in normal *Lamarckiana* or other balanced species.

Translocation B also represents an exchange of ends between chromosomes II and III; but it forms four kinds of gametes in more nearly equal numbers than are the various kinds formed by A and C. One may judge that it does not, in general, form a good parallel to the behavior of the *Œnothera* rings. The essential difference between B, on the one hand, and A and C on the other, is that A and C represent exchanges of roughly equal parts, with both breakages near the spindle-fibers; B represents exchange of half of III for a much smaller portion of II, with one of the breakages well away from the spindle-fiber. One may surmise that the *Œnothera* behavior indicates exchanges of equal portions between chromosomes—very likely of approximately half-chromosomes.

Cleland has described the method of reduction in *Œnothera* rings in detail. It appears that there are fairly numerous irregularities, many of which must produce gametes having more or less than the normal haploid complement of genes; on the translocation view this applies also to the gametes that receive seven chromosomes, some of which were adjacent in the ring. Such gametes are evidently (as has often been pointed out) the ones that appear as shriveled pollen-grains or aborted ovules in the balanced forms of *Œnothera*. In the *Drosophila* translocations these gametes are functional, though they give inviable zygotes unless they meet, at fertilization, gametes with the converse deficiencies and duplications. This difference is, of course, to be attributed to the relatively insignificant duration of the haploid stage in animals as compared to its longer and more complicated development in seed-plants. The gametes of animals are carried through to fertilization by the effects of the genes present before maturation; in plants the genes of the haploid generation itself come into play, and when they are too abnormal the gamete is not properly formed.

Darlington (1929) has suggested that the chromosome rings of *Œnothera* and other forms result from conjugation of like parts of chromosomes, in cases where reciprocal translocation has occurred. The conjugation is like that represented in Diagram 4, A and C, of this paper. As the chromosomes shorten and thicken they separate at their middles, but retain the terminal attachments. The somatic pairing observed in translocations A and C may be taken as favoring this view. The cytological observations on *Œnothera* are not adequate to show whether or not such an origin is probable for the rings. Håkansson (1928) and Weier (1930) have studied the stages near "second contraction," but similar observations made by Emerson (1929) on a haploid plant indicate that this is not the critical stage. Earlier stages have not thus far been found to be decipherable.

The genetic evidence on *Œnothera* speaks strongly for the occurrence of occasional crossovers within rings, for it is difficult to account in any other satisfactory manner for the production of such races as the sulfur-flowered *biennis* or *suaveolens*. These races do not differ from the parent races, either genetically or in their ring configurations, except in being homozygous for the recessive sulfur gene—for which both parents were balanced heterozygotes. The evidence is not so complete, but the probability is that the nanella types of *Lamarckiana* and *biennis* are equally closely similar to the balanced parent races.

One difficulty has always been encountered in picturing the origin of such a balanced condition as that of most of the Œnotheras: namely, how did the lethals, which alone make possible the persistence of such systems, come to be incorporated? The work on *Drosophila* translocations serves to simplify this problem somewhat, since it has been found (Dobzhansky, 1929*b*, this paper) that translocations in general are lethal. One may suppose, then, that the chromosome rings of *Œnothera* were endowed with lethals (in one of their component halves at least) at their very beginnings. If the original *rubens*, for example, was of sufficient selective value to survive, it probably was also lethal from the start, and so was viable only in combination with some partner that was free from that lethal, *i.e.*, only when in a "complex-heterozygote," a ring-forming combination.

It may be pointed out that all the published data on the configurations formed by various combinations of *Œnothera* complexes ("genoms") (see especially Cleland, 1928; Cleland and Oehlkers, 1929; Håkansson, 1928) are consistent with the translocation interpretation. Thus, for example, the complexes *stringens* and *flavens* when combined give a ring of four chromosomes and five pairs. The five pairs are evidently alike (in sufficient genes to control their conjugation), while two chromosomes of *stringens* are each homologous at one end to one of *flavens*, and at the other end to another one of *flavens*. It follows that *flavens* and *stringens*, when combined with other complexes, can differ at most in the disposition of two chromosomes. This is, in fact, the case: with *albicans* they both give a ring of 12 and a pair; with *deprimens*, *stringens* gives a ring of 14 and *flavens* gives a ring of 12 and a pair; with *velans*, *stringens* gives a ring of 6, a ring of 4, and two pairs; *flavens* gives two rings of 4 and three pairs; with *gaudens*, *stringens* gives a ring of 14, *flavens* gives a ring of 12 and a pair.

The analysis has been carried much further than this by Cleland and Blakeslee (1930). Investigations are now in progress in this laboratory (by Emerson and Sturtevant) that should yield extensive tests as to the adequacy of the scheme and should serve to correlate much of the known genetics of *Œnothera* with it. No discordant results have yet been obtained.

SUMMARY

(1) Five translocations (A, B, C, D and E) are described, all involving chromosomes II and III, the first four produced by X-ray treatment.

(2) Translocations A and C represent cases in which chromosomes II and III both broke very close to their spindle-fibers, and the two left halves then reunited, as did the two right halves. That is they are reciprocal translocations, involving an exchange of half-chromosomes.

(3) Translocation B is also reciprocal, the right half of III being exchanged for the terminal section (aristaless to black) of the left half of II.

(4) Translocation D was not analyzed, the flies that carried it being so weak and abnormal as to make analysis impossible.

(5) Translocation E involves the removal of the extreme left end of II (aristaless to dachs), and its attachment at the locus of hairy, near the middle of the left limb of III.

(6) Translocations A, B, C, and E are all lethal in homozygous condition.

(7) In flies heterozygous for these translocations the crossing over is in general reduced in every limb of chromosomes II and III that is directly involved. The reduction is present (though not extreme) in both limbs of both chromosomes in translocations A and C.

(8) When inverted sections are introduced in the non-translocated II of such heterozygous flies, some or all of the reduction in III-chromosome crossing over disappears. Similarly, inverted sections in III cause the disappearance of some or all of the reduction in II-chromosome crossing over.

(9) The degree of independence in the segregation of chromosomes II and III was studied by mating together males and females heterozygous for the same translocation.

(10) In A and C the great majority of the gametes belong to two classes that result from one type of segregation, and these gametes each receive one and only one full complement of genes. Two other types of segregation do occur, but less often.

(11) In translocation B only two types of segregation occur. The normal II and the composite made up of more than half of II plus right half of III always pass to opposite poles, and so do the other two chromosomes; these two events are not independent, more than half of the gametes receiving one and only one full set of genes. There are, however, more exceptional gametes than in the cases of A and C.

(12) In the case of translocation E, every gamete receives a single chromosome III, half of these normal and half with attached fragment of II; half of them get a normal II and half get a deficient II. The four resulting types of gametes occur in equal numbers or very nearly so.

(13) Cytological study shows no difference between translocation E and wild type. In the case of B one unusually long chromosome and one unusually short one are present. In A, B and C the somatic pairing is definitely different

from that of wild type, and is such as to indicate that like regions tend to lie side by side, rather than like chromosomes (as wholes).

(14) The bearing of the results on the nature of synapsis, reduction, and crossing over is pointed out.

(15) The results are discussed in connection with Belling's interpretation of *Œnothera* genetics and cytology. It is concluded that translocations A and C furnish direct proof for the existence of such a mechanism as is required to fit the *Œnothera* data.

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III

TWO NEW ATTACHED-X LINES OF DROSOPHILA MELANOGASTER, AND FURTHER DATA ON THE BEHAVIOR OF HETEROZYGOUS ATTACHED-X's

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With one text-figure

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TWO NEW ATTACHED-X LINES OF DROSOPHILA MELANOGASTER, AND FURTHER DATA ON THE BEHAVIOR OF HETEROZYGOUS ATTACHED-X's[1]

ORIGIN OF THE TWO NEW ATTACHED-X STOCKS

From the mating $\frac{B}{f\ B\ fu}$ ♀ × f B fu ♂ a single wild-type male was obtained (June 23, 1923, see Sturtevant, 1925, 121-122). This male was unexpected, since all other bar reversions from this mating were forked or fused. Accordingly he was tested by mating to attached-X yellow females (L. V. Morgan, 1922). There were produced 59 yellow females, 85 wild-type males, 5 wild-type females, and 38 "super-females" (3 X's, 2 sets of autosomes, no mutant characters).[2] The yellow females and wild-type males were to be expected if the parents were as supposed, the father being not-bar. The 5 wild-type females were presumably due to separation of the attached-X's of the mother, and were therefore $\frac{+}{y}$ in constitution. All were tested, and 4 of them conformed to this expectation. The fifth, mated to a wild-type brother, gave 48 wild-type females, 69 wild-type males, and 1 (wild-type) super-female. This result showed that the mother carried two paternal (wild-type) X's, which were later found to be attached. This line will be referred to as attached-X number 3 (number 1, L. V. Morgan, 1922; number 2, Anderson, 1925).

Four matings were made of yellow (attached-X, line 1) females, from the original mating above, by some of their 85 wild-type brothers. These produced the following results:

Culture	y ♀	+ ♀	super-♀	+ ♂	y ♂
1,3443.....	93	0	16	128	0
1,3451.....	33	0	2	37	0
1,3460.....	63	0	11	65	1
1,3471.....	51	1	9	65	0

The one yellow male must have arisen through separation of the attached-X's of his mother, and it was probable that the one wild-type female arose in the same way. However, when she was mated to an unrelated forked bar male, she produced 77 wild-type females and 68 forked bar males. Tests of descendants (and cytological study) verified the conclusion that this female again had 2 wild-type paternal X's that were attached. This line will be referred to as attached-X number 4.

[1] The work on which this paper is based was supported by Carnegie Institution of Washington.

[2] The high frequency of super-females here and in some of the other cultures of this stock is unusual. The frequency with which such flies survive is known to be much affected by modifying genes and is also influenced by temperature (see Dobzhansky, 1928).

Three more generations were reared from yellow females × wild-type males of the original line, with the production of 657 yellow females, 2 wild-type females, 79 (wild-type) super-females, 714 wild-type males, and 1 yellow male. The two wild-type females were both tested, and both proved to be "breaks," *i.e.*, +/y with the X's not attached. I have not met with any further certain cases of sperm that carried one set of autosomes and two X's, though other workers have occasionally found them (*cf.*, L. V. Morgan, 1925).

As suggested before (Sturtevant, 1925), it is not improbable that the original wild-type male, with which these cultures began, was not produced by his supposed parents, but arose through contamination. Another clue lies in the evidence, obtained somewhat later by Dr. E. Gabritschevsky, that the attached-X's of line number 4 both carry a bobbed allelomorph. It seems probable that this allelomorph was present in the original male, but it was never detected in the bar experiments from which he came.[1]

HISTORY OF ATTACHED-X, LINE 3

The results obtained from line 3 (including the original culture) are shown in table 1.

TABLE 1—+ ♀ (*line 3*) × *various* ♂♂

Males used	+♀	Super-♀	Patroclinous ♂	Matroclinous ♂ ("break")
Yellow prune	129	25	134	1
Bar (mostly, also forked)	863	16	889	5
Wild-type	290	12	320	

The super-females from bar fathers were all bar, as expected. This mating also produced 5 heterozygous bar females, 4 of which were tested and found to be B/+, evidently due to separation of the X's of the line 3 mothers. The 889 bar males of the table include the original infra-bar mutant (see Sturtevant, 1925, 125).

The totals (males from yellow prune mating and both sexes from bar mating) show that 11 breaks occurred among 1897 offspring. All the separate-X eggs should survive, while half of the eggs that carried attached-X's before maturation give super-females or YO (inviable) zygotes. Accordingly the indicated frequency of separations is $11 \div ([1886 \times 2] + 11) = 0.29$ per cent.

HISTORY OF ATTACHED-X, LINE 4

Wild-type females of the original line 4 were mated only to bar males (usually these were also forked). There were produced 826 wild-type females, 3 super-females (slight bar), 2 heterozygous bar females, 872 bar males, 0 wild-type males. The 2 heterozygous bar females (both produced by one

[1] It is still possible that bobbed was present in the not-forked not-fused chromosome of that strain, since in that case only occasional fused-bobbed crossover males would produce bobbed daughters, and the chance is high that such crossovers did not happen to be used. It should be added that the experiments of Bridges and others (largely unpublished) show that bobbed allelomorphs occur in many stocks, often being unnoticed because of the presence of a dominant wild-type allelomorph in the normal Y (Stern, 1927).

mother) were tested; one was B/+, due to a break, while the other was triploid (to be discussed in the next section).

There was accordingly 1 break among the 1699 offspring (excluding the triploid and the super-females), indicating a primary frequency of 0.06 per cent of breaks among the unreduced eggs of line 4 females.

Cytological study of a female of line 4 (obtained in the heterozygous series to be described below) showed the chromosomes to be quite like those figured by L. V. Morgan (1922) for line 1.

TRIPLOIDY IN LINE 4

A wild-type attached-X female of line 4, mated to 2 forked bar males, produced a heterozygous bar female. This female was mated to unrelated yellow prune males (culture 13802) and produced 17 heterozygous bar females, 16 wild-type females, 13 forked bar males, 1 yellow prune male, 8 heterozygous bar intersexes, and 9 wild-type intersexes. This result, together with extensive tests of the descendants of 13802, make it clear that the mother of that culture was a triploid, with two attached wild-type X's and a free forked bar X. Data from similar females, with line 1 attached-X's have already been published by L. V. Morgan (1925). The data from the present case do not add materially to that account and are therefore not presented. The 13802 strain was, however, used to obtain diploid attached-X females heterozygous for a variety of sex-linked genes, and it is with the results from such females that the present paper is chiefly concerned.

ORIGIN OF ATTACHED-X SERIES HETEROZYGOUS FOR X-PLE

A triploid female of the line 4 series had attached-X's (one of which was wild-type, the other apparently garnet), and carried a free X-ple chromosome received from her father. This female was mated to bar males and produced 25 bar females (some of them 3n), 45 not-bar females (all 2n, many showing parts of X-ple, especially garnet), 24 bar males, 18 not-bar males, and 12 intersexes. Five of the not-bar females were tested, and all, as expected, proved to be diploids with attached-X's. One of these (culture 14308) was mated to miniature males. There resulted 2 super-females, 77 miniature males, and 78 females belonging to the following classes: 37 wild-type, 1 f, 1 g, 4 g f, 2 v, 2 v g f, 1 ct v, 1 ct v g, 3 cv ct v, 1 cv ct v g, 1 cv ct vg f, 1 ec, 3 ec cv, 1 ec cv g f, 1 ec cv ct f, 2 sc cv ct, 2 sc cv ct v, 2 ec cv ct v g, 8 sc, 2 sc g f, 1 sc v g, 1 sc v g f.

Evidently the female of 14308 was an attached-X heterozygous for all of X-ple. Analysis of her daughters indicates that she did not carry one wild-type X and one X-ple one. Of the 13 forked daughters, 11 were also garnet; of the 17 garnets 9 were also vermilion; 4 had all three of these characters. We may conclude (on comparison with results from other types of mothers) that v g and f were carried in the same X; similar analysis leads to the conclusion that that same X also carried ct, cv and ec, but not sc. Of the 12 scute daughters none were echinus, crossveinless, or cut. Two were vermilion, four were garnet, and three were forked; but it is clear that such relations are more significant as between loci known to lie close together (as are sc, ec and cv, but not sc and g or v). We may conclude that female 14308 was $\frac{\text{sc}}{\text{ec cv ct v g f}}$ in constitution.

The results obtained from one of her daughters (in culture 14424) are of interest in this connection. This female, mated to double-bar males, gave 88 double-bar sons and the following 77 daughters: 52 wild-type, 3 g f, 1 v, 1 v g, 1 v g f, 1 cv ct, 1 cv ct v, 1 ec, 1 ec cv ct v g, 5 sc, 5 sc ec, 5 sc ec cv ct. These results differ strikingly from those above in one respect only: 10 of the 15 scutes were also echinus, and 5 of them were crossveinless and cut. Female 14424 was $\frac{+}{\text{sc ec cv ct v g f}}$.

Similar analysis of the results given by each tested female in the line that was heterozygous for all of X-ple has made it possible to determine the makeup in every case where a reasonable number of daughters was produced. Since forked appears in only about 5 per cent of the daughters of a mother heterozygous for forked, it is evident that, through chance alone, the forked character may fail to appear in a small family. This source of error is present in the data as given; probably some of the females supposed to be homozygous not-forked (and therefore not recorded) really were heterozygous for forked. On the other hand, many females that gave less than 50 daughters, without any forked, have been left out of the tables as doubtful, while some females, with less than that number of offspring (that did include forked), have been included. There is thus a possible error in each direction in dealing with this locus, though this is probably small.

There are 64 ($= 2^6$) possible different arrangements of the genes in females heterozygous for X-ple. Owing to the frequency of crossing over, it was not possible to keep the attached-X strain to any one of these types, as would have been desirable for further analysis and as was done by Anderson when working with a shorter heterozygous section. As a result, 61 of the 64 possible types were found. The daughters produced (excluding breaks and super-females) are shown in Table 2.

The total frequencies for each homozygous recessive mutant type obtained are as follows:

	N	sc	ec	cv	ct	v	g	f
Table 2	24,247	4157	4006	3862	4028	3609	2508	1232
Anderson, '25	4,344	.....	.....	.....	672	.....	414	226
L. V. Morgan, '25	1,238	201	213	193	.....	153	137	64
Per cent: Table 2	.....	17.1	16.5	15.9	16.6	14.9	10.3	5.1
Anderson	.....	.....	.....	.....	15.5	.....	9.5	5.2
L. V. Morgan	.....	16.7	17.3	15.6	.....	12.4	11.1	5.2
Total	.....	17.1	16.5	15.9	16.4	14.8	10.1	5.1

TABLE 2—*Offspring of attached-X females heterozygous for all of X-ple. Numbers in first column indicate number of females of the types concerned, that were studied*

+ / sc ec cv ct v g f	+	f	g	g f	v	v g	v g f	ct	ct v	ct v g	ct v g f	cv	cv ct	cv ct v	cv ct v g	cv ct v g f	ec	ec cv	ec cv ct	ec cv ct v	ec cv ct v g	ec cv ct v g f	sc	sc v g	sc ec	sc ec cv	sc ec cv ct	sc ec cv ct v	sc ec cv ct v g	sc ec cv ct v g f		Total
13	614	1	1	4	6	8	9	4	4	6	5	2	7	12	10	3	1	2	4	5	9	3	27	2	36	18	47	16	9	5		880
f / sc ec cv ct v g	+	f	v	v g	ct v g	cv ct	ec cv ct	ec cv ct v	ec cv ct v g	sc	sc ec	sc ec f	sc ec cv	sc ec cv ct																		
2	121	1	1	2	3	3	2	2	1	3	10	1	3	2																		155
g f / sc ec cv ct v	+	f	g	g f	v	ct	ct v	cv	cv ct	cv ct v	ec cv	ec cv ct	ec cv ct v	sc	sc g	sc v	sc ec	sc ec g f	sc ec v	sc ec cv	sc ec cv ct	sc ec cv ct v										
13	515	2	56	38	27	2	30	1	5	28	2	7	28	16	1	2	20	3	1	22	28	39										873
v / sc ec cv ct g f	+	f	g	g f	v	v f	ct	ct g	cv ct	cv ct g	cv ct g f	ec cv ct	ec cv ct g	ec cv ct g f	sc	sc g f	sc ec	sc ec cv	sc ec cv v	sc ec cv ct	sc ec cv ct g	sc ec cv ct g f										
6	248	2	9	14	78	1	6	7	6	6	7	4	5	2	4	1	22	13	1	20	1	4										461
v f / sc ec cv ct g	+	f	g	v	v f	ct g	cv ct	cv ct g	ec cv ct	ec cv ct g	sc	sc ec	sc ec cv	sc ec cv ct	sc ec cv ct g																	
2	73	2	2	18	7	2	4	1	1	2	2	7	5	8	1																	135
v g / sc ec cv ct f	+	f	v	v g	ct	cv	cv ct f	ec cv ct	ec cv ct f	sc	sc ec	sc ec cv	sc ec cv ct																			
1	46	1	2	8	1	1	1	2	1	5	3	3	3																			77
v g f / sc ec cv ct	+	f	g	g f	v	v g	v g f	ct	cv ct	ec cv	ec cv ct	sc	sc ec	sc ec cv	sc ec cv ct																	
4	189	1	1	1	17	20	11	8	11	2	11	6	8	7	18																	311

TABLE 2—*Continued*

ct / sc ec cv v g f / 4	+	f	g f	v	v g	v g f	ct	cv	cv v	cv v g	cv v g f	ec cv	ec cv v	ec cv v g	sc	sc ec	sc ec cv	sc ec cv g f	sc ec cv v	sc ec cv v g												Total
	121	1	2	4	4	3	44	3	4	2	1	1	2	2	7	6	17	1	3	1												229
ct f / sc ec cv v g / 4	+	f	v	v g	ct	ct f	cv	cv v	cv v g	ec	ec v	ec cv	ec cv v	sc	sc v g	sc ec	sc ec cv	sc ec cv v	sc ec cv v g														195
	109	8	4	5	30	4	1	2	2	1	1	1	2	2	1	5	9	4	4														
ct g / sc ec cv v f / 4	+	f	g	v	v f	ct	ct f	ct g	cv	cv v	ec	ec cv	ec cv v	sc	sc v	sc ec	sc ec f	sc ec cv	sc ec cv v	sc ec cv v f													249
	96	5	17	15	15	36	1	24	2	6	1	2	4	3	1	6	1	8	5	1													
ct g f / sc ec cv v / 4	+	f	g	g f	v	ct	ct g	ct g f	cv	cv v	ec cv	ec cv v	sc	sc g	sc ec	sc ec cv	sc ec cv v																171
	79	1	3	8	10	23	8	4	1	3	4	2	5	1	4	10	5																
ct v / sc ec cv g f / 7	+	f	g	g f	v	ct	ct v	cv	cv f	cv g	cv g f	ec	ec ct	ec cv	ec cv g	ec cv g f	sc	sc g f	sc v	sc ec	sc ec g f	sc ec v	sc ec cv	sc ec cv g	sc ec cv g f								367
	170	3	10	17	13	16	52	4	1	4	6	1	1	13	4	1	11	2	1	13	1	1	20	1	1								
ct v f / sc ec cv g / 14	+	f	g	v	v f	ct	ct v	ct v f	cv	cv g	ec cv	ec cv g	sc	sc f	sc g	sc v f	sc ct v	sc ec	sc ec f	sc ec g	sc ec v f	sc ec cv	sc ec cv g										728
	349	14	44	15	7	46	68	15	14	15	17	10	22	1	3	1	1	15	1	2	1	56	11										
ct v g / sc ec cv f / 11	+	f	g	v	v g	ct	ct g	ct v	ct v g	cv	cv f	cv g	ec cv	ec cv f	sc	sc v g	sc ec	sc ec f	sc ec v g	sc ec cv	sc ec cv f												573
	289	15	10	5	14	41	1	34	39	20	1	1	9	5	13	1	22	1	1	48	3												
ct v g f / sc ec cv / 4	+	f	g	g f	v	v g	v g f	ct	ct v	ct v g	ct v g f	cv	cv g	ec cv	sc	sc g	sc ec	sc ec cv	sc ec cv g	sc ec cv g f													281
	162	1	10	2	3	3	3	10	10	12	2	9	2	11	7	1	7	23	2	1													

TABLE 2—*Continued*

cv / sc ec ct v g f	+	f	g	g f	v g	v g f	ct	ct v	ct v g	ct v g f	cv	ec ct	ec ct v	ec ct v g	ec ct v g f	sc	sc ec	sc ec ct	sc ec ct v	sc ec ct v g f	Total
3																					
	98	2	2	2	3	4	1	2	6	2	25	1	1	3	1	2	9	16	6	1	187
cv f / sc ec ct v g	+	f	g	g f	v g	ct	ct v	ct v g	cv	cv f	cv g	ec	ec ct	ec ct v	ec ct v g	sc	sc ec	sc ec ct	sc ec ct v	sc ec ct v g	
5																					
	132	10	3	1	6	1	7	5	46	10	1	1	7	6	7	12	19	16	9	4	305
cv g / sc ec ct v f	+	f	g	v	v f	ct	ct v	ct v f	cv	cv g	ec	ec g	ec ct	ec ct v	ec ct v f	sc	sc g	sc v f	sc cv g	sc ec	sc ec g	sc ec v	sc ec ct	sc ec ct g	sc ec ct v	sc ec ct v f	
16																											
	413	4	43	17	19	10	41	21	121	40	8	1	7	17	3	35	1	1	1	59	3	1	38	1	21	2	928
cv g f / sc ec ct v	+	f	g	g f	v	ct	ct v	cv	cv g	cv g f	ec	ec ct	ec ct v	sc	sc ec	sc ec v	sc ec ct	sc ec ct v									
10																											
	313	2	14	18	7	10	34	75	10	10	1	2	14	27	39	1	23	15									615
cv v / sc ec ct g f	+	f	g	g f	v	ct	ct g	ct g f	cv	cv v	ec	ec ct	sc	sc ec	sc ec ct	sc ec ct g											
5																											
	171	1	4	4	12	9	6	2	25	29	3	8	12	16	28	6											336
cv v f / sc ec ct g	+	f	g	v	v f	ct	ct g	cv	cv v	cv v f	ec	ec ct	ec ct g	sc	sc ec	sc ec ct	sc ec ct g										Total
5																											
	123	3	13	5	3	3	13	27	10	5	2	7	2	5	16	10	7										254
cv v g f / sc ec ct	+	g	v	v g	v g f	ct	cv	cv v	cv v g	cv v g f	ec	ec ct	sc	sc ec	sc ec ct												
2																											
	48	2	2	2	4	7	11	4	2	1	2	1	7	6	9												108
cv ct / sc ec v g f	+	f	g	g f	v	v g	v g f	ct	cv	cv f	cv v	cv ct	ec	ec g f	ec v	ec v g	ec v g f	sc	sc g	sc ec	sc ec v	sc ec v g					
8																											
	287	1	3	3	15	28	20	16	9	1	1	39	10	1	6	4	3	19	1	59	12	7					595

TABLE 2—*Continued*

cv ct f / sc ec v g 2	+	f	g	v	v g	ct	ct f	cv	cv ct	cv ct f	ec	ec v	ec v g	sc	sc ec	sc ec f	sc ec v							Total
	173	2	5	7	12	5	1	6	18	3	4	1	3	7	14	1	6							173
cv ct g / sc ec v f 9	+	f	g	v	v f	ct	ct g	cv	cv g	cv ct	cv ct g	ec	ec v	ec v f	sc	sc g	sc ec	sc ec f	sc ec v	sc ec v f	sc ec v g			
	210	4	16	38	13	9	8	14	1	38	6	6	7	3	17	2	33	3	12	2	1			443
cv ct g f / sc ec v 5	+	f	g	g f	v	ct	ct g	ct g f	cv	cv f	cv v	cv ct	cv ct g	cv ct g f	ec	ec v	sc	sc ec	sc ec g	sc ec v				
	176	4	13	5	31	2	4	4	6	1	1	49	13	5	2	9	13	37	1	11				387
cv ct v / sc ec g f 5	+	f	g	g f	v	ct	ct v	cv	cv ct	cv ct v	ec	ec g	ec g f	sc	sc g f	sc ec	sc ec f	sc ec g f						
	183	3	8	18	17	1	13	13	25	24	11	1	2	15	2	41	1	2						390
cv ct v f / sc ec g 10	+	f	g	v	v f	ct	ct v	cv	cv ct	cv ct v	cv ct v f	ec	ec g	sc	sc f	sc g	sc ec	sc ec g	sc ec v					
	330	3	49	12	9	2	9	21	30	41	5	24	11	26	2	1	80	12	1					668
cv ct v g / sc ec f 1	+	f	g	v	v g	ct	ct v	ct v g	cv	cv ct	cv ct v	cv ct v g	ec	sc	sc f	sc ec								
	42	3	1	1	1	1	1	2	3	4	1	1	3	3	2	12								81
cv ct v g f / sc ec 4	+	f	g	g f	v	v g	v g f	ct	ct v	ct v g	ct v g f	cv	cv ct	cv ct v	cv ct v g	cv ct v g f	ec	sc	sc ec					
	159	1	1	6	2	3	1	3	2	2	2	8	16	8	9	6	17	12	34					292
ec / sc cv ct v g f 8	+	f	g	g f	v	v g	v g f	ct v	ct v g	ct v g f	cv ct	cv ct v	cv ct v g	cv ct v g f	ec	sc	sc g f	sc ct v g	sc cv	sc cv v g	sc cv ct	sc cv ct v	sc cv ct v g	
	259	1	2	9	2	5	6	2	6	3	6	8	8	8	107	23	1	1	15	1	21	3	5	502

TABLE 2—*Continued*

ec f / sc cv ct v g 8	+	f	g	v	v g	ct	ct v	ct v g	cv	cv ct	cv ct v			cv ct v g	ec	ec f	ec v	ec ct v	sc	sc f	sc ct v g	sc cv	sc cv ct	sc cv ct v	sc cv ct v g	Total
	281	17	2	6	18	5	7	9	5	7	12			12	79	4	1	1	45	1	1	9	10	9	4	545
ec g / sc cv ct v f 9	+	f	g	v	v f	ct	ct v	ct v f	cv	cv ct	cv ct v	cv ct v f	ec	ec f	ec g	sc	sc g	sc v f	sc cv	sc cv ct	sc cv ct v	sc cv ct v f					
	174	6	28	16	11	2	14	3	4	13	22	8	49	1	13	25	1	1	10	15	13	1				430
ec g f / sc cv ct v 9	+	g	g f	v	ct	ct v	cv ct	cv ct v	ec	ec g	ec g f	ec v	sc	sc g	sc cv	sc cv ct	sc cv ct v									
	202	16	24	8	1	13	4	17	52	6	1	2	28	1	11	13	6									405
ec v / sc cv ct g f 6	+	f	g	g f	v	ct	ct g	ct g f	cv	cv ct	cv ct g	cv ct g f	ec	ec g	ec v	sc	sc v	sc cv	sc cv ct	sc cv ct g	sc cv ct g f						
	181	1	13	9	46	5	3	3	1	8	5	6	27	1	34	32	3	11	24	2	1					416
ec v f / sc cv ct g 16	+	f	g	v	v f	ct	ct g	cv	cv g	cv ct	cv ct g	ec	ec g	ec v	ec v f	sc	sc f	sc g	sc v	sc v f	sc cv	sc cv ct	sc cv ct g				
	386	11	39	61	24	14	12	2	1	32	28	102	4	43	13	62	1	5	6	4	20	37	9				916
ec v g / sc cv ct f 6	+	f	g	v	v g	ct	ct f	cv	cv ct	cv ct f	ec	ec f	ec v	ec v g	sc	sc f	sc g	sc cv	sc cv ct	sc cv ct f							
	218	5	5	12	33	11	2	2	34	4	60	1	18	11	38	1	1	8	21	2							487
ec v g f / sc cv ct 1	+	g f	v	v g	v g f	ct	cv ct	ec	ec v	ec v g f	sc	sc v g	sc cv	sc cv ct													
	39	2	3	3	5	1	6	11	1	1	3	1	1	3													80
ec ct / sc cv v g f 4	+	f	g f	v	v g	v g f	ct	cv	cv v	cv v g	cv v g f	ec	ec ct	sc	sc f	sc cv	sc cv f	sc cv v	sc cv v g	sc cv v g f							
	120	1	1	4	7	6	15	4	6	5	3	21	28	20	1	24	1	3	5	5							280

TABLE 2—*Continued*

ec ct f / sc cv v g 3	+	f	g	v	v g	ct	ct f	cv	cv g	cv v	cv v g	ec	ec g	ec v	ec ct	ec ct f	sc	sc f	sc g	sc cv	sc cv v	sc cv v g									Total
	100	1	4	5	12	13	3	4	2	8	14	18	1	1	26	1	19	1	1	23	6	2									268
ec ct g / sc cv v f 6	+	f	g	v	v f	ct	ct g	cv	cv v	cv v f	ec	ec f	ec g	ec ct	ec ct g	sc	sc f	sc g	sc v	sc v f	sc cv	sc cv v	sc cv v f									Total
	117	3	17	22	5	13	11	9	22	3	21	1	1	24	8	11	1	1	2	1	27	10	2								332
ec ct g f / sc cv v 10	+	f	g	g f	v	ct	ct g	ct g f	cv	cv g f	cv v	ec	ec g f	ec v	ec ct	ec ct g	ec ct g f	sc	sc g	sc v	sc ct g	sc cv	sc cv g	sc cv v								
	210	2	11	17	33	18	12	7	18	1	24	30	1	1	31	10	7	27	1	4	1	23	1	22							512
ec ct v / sc cv g f 12	+	g	g f	v	ct	ct v	cv	cv g	cv g f	ec	ec g	ec g f	ec ct	ec ct v	sc	sc g	sc g f	sc v	sc cv	sc cv f	sc cv g	sc cv g f										
	305	13	26	18	6	32	26	11	8	33	1	2	23	46	46	1	2	2	56	1	4	5									667
ec ct v f / sc cv g 13	+	f	g	v	v f	ct	ct v	ct v f	cv	cv g	ec	ec g	ec v	ec ct	ec ct f	ec ct g	ec ct v	ec ct v f	ec cv	sc	sc f	sc g	sc v f	sc ct v	sc cv	sc cv g						
	352	3	47	15	5	14	44	15	31	34	65	2	3	48	1	1	54	4	1	69	1	2	2	1	90	12						916
ec ct v g / sc cv f 4	+	f	g	v	v g	ct	ct v	ct v g	cv	cv f	ec	ec g	ec ct	ec ct f	ec ct v	ec ct v g	sc	sc f	sc v g	sc cv	sc cv f											
	108	7	2	1	4	3	4	9	21	1	18	1	10	1	8	6	24	2	1	22	1											254
ec ct v g f / sc cv 8	+	g	g f	v	v g	v g f	ct	ct v	ct v g	ct v g f	cv	ec	ec ct	ec ct v	ec ct v g	e c ct v g f	sc	sc v g f	sc ct v	sc cv												
	229	1	5	1	5	4	3	6	11	7	30	39	20	19	11	5	42	1	1	55												495
ec cv / sc ct v g f 1	+	g	g f	v g f	ct	ct v	ct v g	ct v g f	ec	ec cv	sc	sc ct	sc ct v g																			
	29	1	2	2	1	1	1	1	4	8	6	7	1																			64

TABLE 2—*Continued*

ec cv f / sc ct v g 1	+	f	v g	ct v	ct v g	ec	ec g	ec cv	ec cv f	sc	sc ct	sc ct v																		Total
	49	3	2	3	4	3	1	12	1	12	3	2																		95
ec cv g / sc ct v f 8	+	f	g	v	v f	ct	ct v	ct v f	cv	cv g	ec	ec v f	ec cv	ec cv f	ec cv g	sc	sc f	sc ct	sc ct g	sc ct v	sc ct v f										
	17	5	15	8	2	9	32	2	13	3	9	1	38	1	5	49	1	30	1	9	4										407
ec cv g f / sc ct v 12	+	f	g	g f	v	ct	ct v	cv	cv g	cv g f	ec	ec g	ec g f	ec cv	ec cv f	ec cv g	ec cv g f	sc	sc f	sc g	sc g f	sc ct	sc ct g	sc ct v							
	308	2	21	17	25	17	37	6	7	4	28	1	1	83	1	9	5	74	1	1	1	39	1	36							725
ec cv v / sc ct g f 8	+	f	g	g f	v	ct	ct g	ct g f	cv	cv v	ec	ec ct	ec cv	ec cv v	sc	sc g	sc g f	sc v	sc ct	sc ct g	sc ct g f										
	290	1	3	7	22	17	13	6	1	10	10	1	42	31	42	1	1	1	41	6	4										550
ec cv v f / sc ct g 4	+	f	g	v	v f	ct	ct g	cv	cv v	cv v f	ec	ec cv	ec cv v	ec cv v f	sc	sc v	sc ct	sc ct g													
	72	2	3	4	9	14	14	2	4	3	5	8	6	1	20	1	5	2													175
ec cv v g f / sc ct 2	+	g	v g	v g f	ct	cv	cv v	cv v g	cv v g f	ec	ec g f	ec cv	ec cv v	ec cv v g f	sc	sc ct															
	79	1	2	5	13	1	1	1	1	4	1	14	3	2	13	18															159
ec cv ct / sc v g f 7	+	f	g	g f	v	v g	v g f	ct	cv	cv ct	ec	ec g f	ec cv	ec cv ct	sc	sc f	sc g f	sc v	sc v g												
	252	2	2	5	17	23	16	9	1	19	17	1	12	45	79	1	1	14	12												528
ec cv ct f / sc v g 3	+	f	g	v	v g	ct f	cv	cv ct	cv ct f	ec	ec v g	ec cv	ec cv ct	sc	sc g	sc v	sc v g														
	59	4	2	5	13	1	1	5	1	6	2	1	9	20	2	2	3														136

TABLE 2—*Continued*

ec cv ct g / sc v f / 9	+	f	g	v	v f	ct	ct g	cv ct	cv ct g	ec	ec f	ec ct g	ec cv	ec cv ct	ec cv ct g	sc	sc g	sc v	sc v f	sc ct g	sc cv ct										Total
	258	5	16	52	14	7	7	9	3	17	1	1	9	27	5	85	5	16	3	1	1										542
ec cv ct g f / sc v / 1	+	g f	v	ct	cv ct	cv ct g	ec	ec cv	ec cv ct	ec cv ct g	sc	sc v																			
	32	1	10	1	1	3	3	4	7	2	20	3																			87
ec cv ct v / sc g f / 6	+	f	g	g f	v	ct v	cv ct v	ec	ec f	ec g	ec cv	ec cv v	ec cv ct	ec cv ct v	sc	sc g	sc g f	sc v													
	145	1	8	9	10	14	8	10	1	1	6	1	12	19	46	5	4	2													302
ec cv ct v f / sc g / 3	+	f	g	v	v f	ct	ct v	ct v f	cv ct	cv ct v	cv ct v f	ec	ec cv	ec cv g	ec cv ct	ec cv ct v	ec cv ct v f	sc	sc g	sc v												
	83	3	16	1	2	1	3	1	2	6	1	9	6	1	5	7	2	39	2	1											191
ec cv ct v g / sc f / 5	+	f	g	v	v g	ct v	ct v g	cv ct	cv ct v	cv ct v g	ec	ec v g	ec cv	ec cv ct	ec cv ct f	ec cv ct v	ec cv ct v g	sc	sc f	sc g												
	118	10	1	1	9	3	4	1	1	3	13	1	6	14	1	5	3	41	1	2											238
sc / ec cv ct v g f / 15	+	f	g	g f	v	v g	v g f	ct v	ct v g	ct v g f	cv ct	cv ct v	cv ct v g	cv ct v g f	ec	ec v g	ec cv	ec cv g f	ec cv ct	ec cv ct f	ec cv ct g f	ec cv ct v	ec cv ct v g	ec cv ct v g f	sc	sc f	sc g	sc g f	sc v g	sc v g f	sc ct v g f	
	557	2	3	17	9	18	21	15	10	7	9	19	7	8	34	1	29	2	54	1	2	32	24	6	198	1	1	4	1	3	1	1096

NOTE. In the last experiment of page 68, the 14 g, not v, not f flies all came from one of the four cultures concerned. A daughter (that did not carry sc or lc) gave similar results. Presumably there was present some other eye-color resembling garnet.

To these values should be added the following miscellaneous results:

Loci	Obtained by	N	homozygous recessives	Per cent
Yellow.....	L. V. Morgan, '25	1593	302	19.0
Tan.....	Anderson, '25	4544	698	16.1
Lozenge.....	Sturtevant, new data	833	124	14.9
White.....	do do	837	138	16.5
Miniature.....	do do	1013	137	13.5
Bar.....	do do	514	21	4.1

Figure 1 shows these values, plotted against the standard map as a base-line. The value for yellow is obviously too high, as it can not be different from that for scute (there being no crossing over between the two loci). This is perhaps in part a viability effect, due to the fact that, in the experiments concerned, the not-yellow chromosome usually carried many more mutant genes than did the yellow one. The value for lozenge is too low, undoubtedly because lozenge itself has rather poor viability. Crossveinless also gives a value that appears to be too low. This was tested by computing the frequency for ec in all experiments of the type ec cv/+. There were 1712 ec among 10,980 flies, or 15.6 per cent, as compared to 16.5 per cent for all the data. Likewise, cv ct/+ gave 14.4 per cent ct, as against 16.6 per cent for all the data. There can be no doubt, then, that the slight dip in the curve at cv is due to slightly poorer viability of the crossveinless flies. With these exceptions, the curve appears to be smooth and self-consistent.

As Anderson (1925) has shown, loci that give free recombination with the attachment-point of the two X-chromosomes should give 16.7 per cent of homozygosis. This line is drawn in figure 1. Evidently the expectation is reached at or slightly to the right of cut, or within 50 units of the attachment-point. That scute gives a percentage higher than 16.7 is unexpected, and may not be significant. The right-hand portion of the curve is nearly a straight line; if this line is continued it cuts the base-line at about 70—the locus assigned to bobbed, the right-most known locus. It may be noted that Stern (1929) has been unable to get crossing over between bobbed and a fragment of Y-chromosome that is visibly attached to the end of the X.

Another series of data involves the fused gene that lies 2.7 units to the right of f. Fused has poor viability, and its expected frequency of homozygosis is so low that chance alone would be expected frequently to cause it not to appear when present. In fact, it several times failed to appear in one generation but was recovered in a later one. The females used were of the constitution $\frac{+}{\text{f fu}}$; all of the fu daughters found were also f, though f not-fu females were relatively common. This result means that the attachment-point of the two X's is beyond fu; as is also clear from Anderson's (1925) analysis of the significance of the percentage of homozygosis for forked, and from the point at which the projection of the homozygosis curve of figure 1 cuts the base-line.

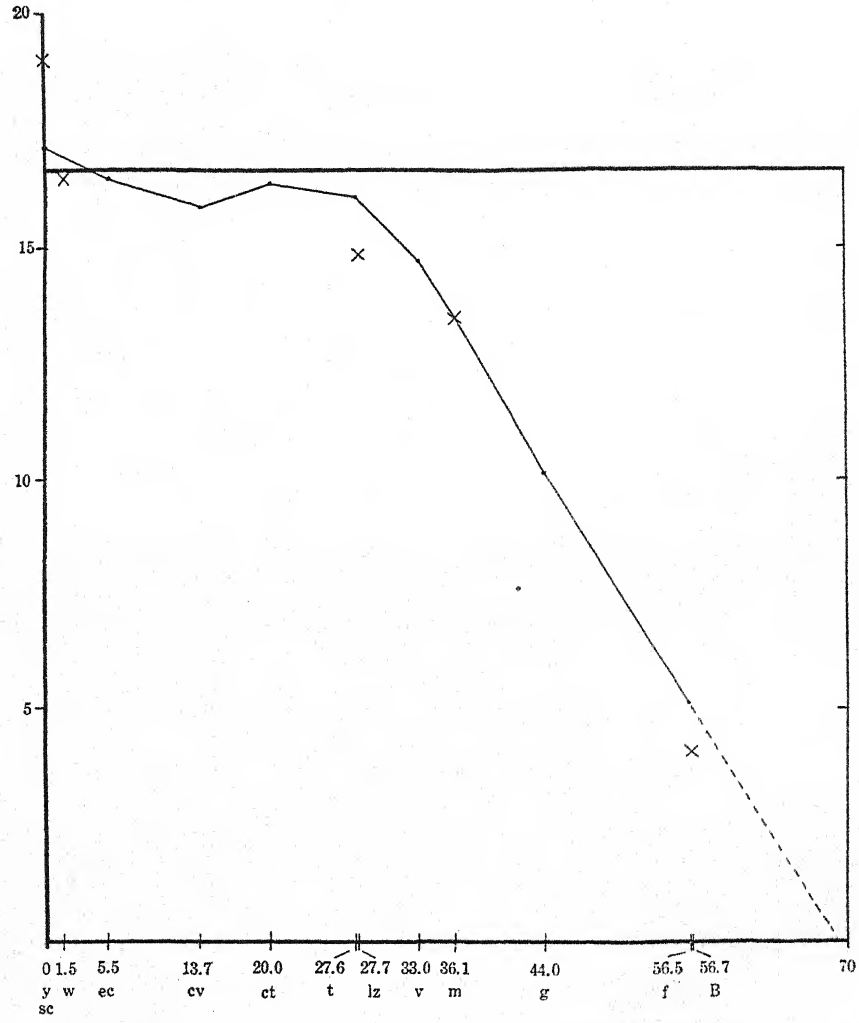

FIG. 1—Curve showing percentages for homozygous recessives produced by attached-X females heterozygous for various sex-linked genes. Base-line of curve is standard map of X-chromosome; line at 16.7 per cent represents frequency expected with random assortment. Values represented by symbol "x" are based on less than 1600 flies each; others, through which curve is drawn, are based on more than 4500 flies each.

TESTS OF DAUGHTERS OF HETEROZYGOUS ATTACHED-X FEMALES

Adequate genetic tests were obtained for the constitution of 629 daughters of mothers heterozygous for all the loci of X-ple. These females do not constitute a random sample of the population from which they came, as the very unusual crossovers were more often tested than were the commoner ones, and wild-type females were bred from in large numbers in order to continue the experiment. No satisfactory method of reducing the data to a random-sample basis has been found. Accordingly the details are not here presented.

TABLE 3—*Types of mothers from which more than 15 wild-type daughters were tested*

Type of mother	All daughters			Tested + daughters			Calculated per cent of all het. for all genes
	Total	+	Per cent that were +	Total	Heterozygous for all genes	Per cent	
sc ec cv ct v g f/+...	880	614	69.8	28	12	42.9	29.8
sc ec cv ct v/g f.....	873	515	59.0	23	13	56.6	33.4
sc ec cv g/ct v f.....	728	349	47.9	24	18	75.0	35.9
sc ec ct v f/cv g.....	928	413	44.5	23	17	73.9	32.9
sc cv ct g/ec v f.....	916	386	42.1	19	16	84.2	35.5
sc cv g f/ec ct v.....	667	305	45.7	18	15	83.3	38.1
sc cv g/ec ct v f.....	916	352	38.4	24	19	79.2	30.4
sc ct v/ec cv g f.....	725	308	42.5	16	13	81.2	34.5
sc/ec cv ct v g f.....	1096	557	50.8	27	21	77.8	39.5
Average.....							34.5

The percentage of daughters that remain heterozygous for all the loci of X-ple can be calculated. Table 3 includes the data from all types of mothers from which as many as 16 wild-type daughters were tested. The percentage for each such type of all daughters that were wild-type is shown, also the percentage of tested wild-type daughters that remained completely heterozygous. From these two values one can deduce (by multiplying the two percentages together and dividing by 100) the percentage of all daughters that remained completely heterozygous. The average of the nine values so obtained is 34.5 per cent.

There were 383 such completely heterozygous daughters tested. These have been arranged in Table 4 according to the kinds of crossing over they represented.

TABLE 4—*Tested daughters that remained completely heterozygous*

(Intervals—sc 1 ec 2 cv 3 ct 4 v 5 g 6 f)

	0	1	2	3	4	5	6	1.2	1.3	1.4	1.5	1.6	2.4	2.5	2.6	3.4	3.5	3.6	4.6	1,3,6	1,2,5,6	Total
N.....	169	28	20	25	55	27	27	1	1	3	4	2	2	6	3	2	1	4	1	1	1	383
Per cent.....	44.2	7.3	5.2	6.5	14.4	7.0	7.0	0.3	0.3	0.8	1.0	0.5	0.5	1.6	0.8	0.5	0.3	1.0	0.3	0.3	0.3	100.0
Per cent of all daughters..	15.4	2.5	1.8	2.2	5.0	2.4	2.4	0.1	0.1	0.3	0.3	0.2	0.2	0.5	0.3	0.2	0.1	0.3	0.1	0.1	0.1	34.6

In the absence of a satisfactory analysis of the crossing over in the remaining 65.5 per cent of the daughters, these data are not very useful in indicating the behavior of the attached-X's.

DETACHMENT OF X'S IN HETEROZYGOUS FEMALES

Females heterozygous for all of X-ple gave several exceptional kinds of offspring. Four triploid females and one intersex (with two maternal X's) were identified. There were also 7 females, not tested genetically, that were probably due to detachment of the X's, though some of these may also have

been triploids. There were 6 males and 10 tested females, certainly due to detachment. One female gave a tested and an untested detached-X daughter, one gave a tested daughter and a son, and a third gave two sons. In view of the extremely low total frequency of detachments this is certainly a higher number of sibs than could result from a random distribution. One may surmise that the detachments sometimes occur in oögonial cells, as suggested by Muller and Dippel (1926). It may be noted that, in the present cases, such an interpretation involves the further assumption that both X's survived after detachment; for the one tested daughter of the first female received a chromosome from her mother that had crossed over between v and g; of the two detached X's recovered from the second female one was a non-crossover and the other was an ec-cv ct-v double crossover; of those from the third female, one was a cv-ct single and the other was a cv-ct ct-v double.

Of the 16 recovered detached X's, 6 were non-crossovers, 4 were single crossovers (2 cv-ct, 2 v-g), and 6 were doubles (1 of each of the following classes: sc-ec ct-v, sc-ec g-f, ec-cv ct-v, cv-ct ct-v, cv-ct g-f, ct-v v-g). As in the case of the detachments studied by Anderson (1925), the numbers here are not large enough to give significant crossover percentages.

Half of the detached-X daughters are expected to carry Y-chromosomes received from their mothers. Among the 10 that were tested, secondary non-disjunction might have been detected in 8 cases, but only 9 offspring were available from one of these, and 51 and 59 respectively from each of two others. Of the remaining 5 females, 2 gave a single exceptional son each—as it happens in each case in a total of 232 offspring. These are not conclusive data, as the two sons concerned might be due to primary non-disjunction. However, one female, due to detachment in a mother homozygous for the f locus, did clearly have a Y, as she gave 3 exceptions among 93 offspring.

MUTATIONS IN THE ATTACHED-X LINE

NOTCH-20

A female of the constitution $\frac{\text{sc}\quad\text{cv}\quad\quad\text{g}}{\text{ec}\quad\text{ct}\quad\text{v}\;\text{f}}$ gave a daughter that had the left wing clearly showing the well-known Notch character, the right wing wild-type. This mosaic female, mated to BB^i males, gave 74 BB^i sons and 45 daughters, 19 of these daughters being Notch and 26 not-Notch. Among the not-Notch females the other characters were: 6+, 3 g, 1 v, 1 v f, 1 ct, 2 ct v f, 1 ec, 7 sc, 3 sc ct, 1 sc ct v. The not-Notch parts of the ovary of the mosaic were, therefore, $\frac{\text{sc}\quad\quad\text{ct}\;\text{v}\;\text{f}}{\text{ec}\;\text{cv}\quad\quad\text{g}}$: *i.e.*, the mosaic developed from an egg that was an ec-cv crossover. The 19 Notch females were: 13+, 3 g, 3 v. Three of the not-Notch daughters were tested. They were found to be, respectively, $\frac{\text{sc}\quad\quad\text{ct}\;\text{v}\;\text{g}}{\text{ec}\;\text{cv}\quad\quad\text{f}}$, $\frac{\text{sc}\quad\quad\text{ct}\quad\text{g}\;\text{f}}{\text{ec}\;\text{cv}\quad\text{g}}$, and $\frac{\text{sc}\;\text{ct}\;\text{v}\quad\text{f}}{\text{sc}\quad\quad\text{g}}$, thus definitely establishing the presence of a portion of the ovary of the mosaic female that did not carry the Notch mutation. Two of the tested Notch daughters were $\frac{\text{N}\;\text{cv}}{\text{sc}\quad\quad\text{ct}}$, one was $\frac{\text{N}}{\text{sc}\quad\text{cv}\;\text{ct}}$, and another was $\frac{\text{N}}{\text{sc}\quad\text{ct}}$ (no crossveinless

recovered, number of daughters only 12)—in all cases neglecting v, g and f. Echinus was not recovered, but was presumably present in the Notch chromosome, close to Notch. The classification here is complicated by the fact that Notch itself produces a somewhat roughened eye, so that Notch echinus would perhaps be overlooked if present in very small numbers. These results show that the Notch portion of the ovary of the mosaic was $\frac{N \quad cv}{sc \quad ct}$, *i.e.*, the genes sc, cv and ct were arranged as in the not-Notch portion of the ovary. Therefore Notch-20 arose without the occurrence of crossing over at or near its locus—a point that is of interest in connection with the well-known fact that the various Notch mutations are due to deficiencies (Mohr, 1919).

The results from this line leave no doubt that homozygous Notch females die, as was to have been expected.

Cut allelomorph—In one strain of attached-X heterozygous for X-ple it was noticed that all of the not-cut females had slightly scalloped wings, the males being wild-type. The occurrence of a detached-X fly in this strain made it possible to establish that the result was due to the occurrence of a mutation to a slight allelomorph of cut in the not-cut chromosome of the strain. The observed slightly scalloped females were heterozygous for the old cut and for the new one, or homozygous for the new one. Males carrying the new cut gene closely resembled these two types of females.

White allelomorph—An attached-X female mated to three B^iB^i males produced 66 B^iB^i sons, one of which had eyes that were barely tinged with color. Tests showed that this male transmitted, in all his X-bearing sperm (73 recovered), a pale allelomorph of white, much like the previously known type tinged.

Dusky allelomorph—An attached-X female, mated to two f BB^i males, produced 65 f BB^i sons, one of which had a very small right wing like that of miniature or dusky, the left wing being wild type. This male was mated to attached-X (line 1) females and produced 124 f BB^i sons; 121 of them with wild-type wings and three with short wings. Two of the latter were tested: one, mated to attached-X females, gave 106 f BB^i sons, all with short wings; the other, mated to a female with X's not attached, gave all normal-winged offspring, the only tested daughter proving to be heterozygous for the new wing-type. Tests showed this to be an allelomorph of the previously known dusky, the new form being rather smaller than the old.

Extra sex-comb—In one attached-X family it was noticed that a few of the males had a small sex-comb, with from 1 to 4 teeth, on the second tarsal segment of one or both front legs. This is the position in which a second sex comb is regularly present in the related species *obscura*. Tests showed the character to be extremely variable, not usually appearing in half of the males that carried the gene concerned. This gene was easily shown to be sex-linked and to lie not far to the left of miniature (3 crossovers in 112 extra-sex-comb males; no crossovers with vermilion in 31 males). Owing to its irregular appearance the character was discarded.

MOSAICS

Three mosaics were found in the experiments with heterozygous attached-X females.

No. 14713—A female $\frac{\text{sc} \qquad \text{v g f}}{\text{ec cv ct}}$ (attached-X's) mated to v f BB^i males gave a mosaic that was wholly ♀, wild type on the left side of the head and thorax and ec cv ct on the right side. The mosaic bred as a female of the same constitution as her mother. The mosaic probably developed from a double-nucleus egg.

No. 16463—A female $\frac{\text{cv} \qquad \text{f}}{\text{ct v g}} \times$ v f B male gave a mosaic that was female throughout, cv f in most of the body, but g and not-f in nearly half of the head and in the right front leg. Since vermilion is not dependable in mosaics (Sturtevant, 1920), and since regions diagnostic for cv and ct were not included in the garnet region, it was not possible to determine the constitution of that region except for the g and f loci and for sex. The simplest interpretation of this mosaic seems to be the double-nucleus one, each of the nuclei concerned having undergone crossing over.

No. 18123—A female $\frac{\text{sc} \quad \text{cv ct g}}{\text{ec} \qquad \text{v f}}$ (with the slight cut allelomorph described above in the ec v f chromosome) × f BB^i male gave a gynandromorph, with the male parts f BB^i and the female parts slight cut (certainly not super-female). Here again a double-nucleus egg seems the simplest interpretation.

L. V. Morgan (1929) has described three mosaics from attached-X mothers. Two were gynandromorphs with maternally derived X's in the female parts and a paternally derived one in the male parts (like No. 18123). These Mrs. Morgan suggests were perhaps due to double-nucleus eggs. The third was wholly female, with the two regions both carrying maternal X's (like No. 14713 rather than No. 16463). This one Mrs. Morgan believes to be very probably due to a double-nucleus egg.

SUMMARY

1. Two new attached-X lines are described, each having arisen from an XX sperm.

2. Triploidy occurred in one of these lines; through its use there was obtained a series of attached-X females heterozygous for sex-linked genes.

3. A curve is presented, showing the frequency of production of daughters homozygous for loci along nearly the entire X-chromosome.

4. This curve, like the earlier ones of Anderson (1925) and L. V. Morgan (1925) that were based on fewer loci and fewer flies, shows approximately 16.7 per cent homozygous recessives for loci from sc (0) to ct (20.0), and approximately a straight-line decrease from vermilion (33.0—14.8 per cent recessives) to bobbed (70.0—0 recessives).

5. New allelomorphs of Notch, cut, white, and dusky, and a sex-linked extra sex-comb, are described. Two of these mutations were present in part of the soma and in part of the germ cells of the original specimens.

6. Three mosaics are described, all probably derived from double-nucleus eggs.

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